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MANUALS

FOR

STUDENTS OF MEDICINE.

ELEMENTS

OF

HUMAN PHYSIOLOGY.

BY

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Dedicated to

W. S. SAVORY, Esq., F.R.S.,

IN PLEASANT MEMORY

OF

MORE THAN FORTY YEARS' SINCERE FRIENDSHIP.

PREFACE.

THE following pages have been written with the object of giving to the student a general outline of the Physiology of Man. The simultaneous appearance of complementary volumes has caused many subjects to be omitted that would otherwise have found a place, and are generally included in text books of physiology. Thus it will be seen that all details of structure are passed over in silence, since they are fully given in Klein's ELEMENTS OF HISTOLOGY. The volume on CLINICAL CHEMISTRY, by Dr. Ralfe, has rendered it unnecessary to mention many organic substances and many tests for organic substances that are usually given. All descriptions of instruments and methods of procedure in practical physiology have been omitted, since they will be found in Dr. M'Gregor-Robertson's work on PHYSIOLOGICAL PHYSICS; and lastly, the appearance of Prof. Bell's treatise on COMPARATIVE ANATOMY AND

Physiology has led to the exclusion of many references to Animal Physiology.

It need hardly be stated, then, that the five volumes should be read together; and if the student has mastered them thoroughly, he will, it is hoped, have acquired a sound basis for the future practice of his profession.

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Human Physiology.

CHAPTER I.

INTRODUCTORY—GENERAL COMPOSITION OF THE BODY.

Human physiology is a branch of biology, and treats of the purposes and functions of the body, and of its several parts. It rests upon anatomy, which naturally includes histology, and upon physics and chemistry. The more accurate our knowledge of these three sciences the better will be our physiology. If, for example, we turn our attention to the physiology of the circulation, we require to know the cause of the circulation of the blood, the course it follows, the speed with which it is accomplished, the action of the heart, the use of its several parts, the circumstances which affect the frequency and force of its action, the quantity of blood it discharges at each beat, the pressure which the blood exerts against the walls of the vessels, the composition of the blood in different parts of its course, and a hundred other points. But to know them properly it is necessary first to know the structure of the heart; its several openings and the valves which guard them; the structure and arrangement of the vessels. This is taught by the anatomist. Then the movement of fluids in closed tubes, the transmission of waves in elastic tubes, and the influence of their resilience, are taught by the physicist, while the chemist teaches us the mutual relations of gases and the blood. The same holds good with the phenomena of respiration and of digestion, with those of

the nervous system and of generation. In all instances we must first know the structure of the organ, then its physics, then its chemistry, before its physiology can be fully understood.

The term *vital phenomena*, applied to the actions which take place in the living body, is correct enough in one sense, but misleading in another. It is right in so far that the course of events in the living body differs from that in the dead, and may, therefore, appropriately be termed vital as a whole; but it is misleading, because it suggests that these events are dependent on some occult and wonderful power, and that they are not the result of the same chemical and physical laws, acting only under different conditions, as those which operate on the dead body. A single illustration will suffice to show the essential identity of vital and non-vital phenomena. A limb shall form part of a healthy living body, and be the seat of vital processes. Blood circulates through it, carrying oxygen to the tissues, which seize upon it, and give in exchange carbonic acid gas. Its several tissues undergo continual change, their molecules are being constantly broken down and removed, and they as constantly abstract nutritive particles from the circulating fluids and effect their own repair. All this is vital; but tie a ligature tightly round it, and with the alteration of the conditions the phenomena at once change their character. The blood no longer circulates, oxygen ceases to be brought to the tissues by the blood, and has but little access from without. The products of decomposition remain in the place where they are found, and soon other living beings prey on the tissues, which are no longer capable of resisting their attacks; putrefactive changes are established, and the complex organic compounds of which they are formed revert, as they did during life, to the simple planes of chemical constitution represented by water, carbon dioxide, and

ammonia, from which they were originally built up. The results are similar in both cases; the essential difference is that in life the conditions are adapted for the renewal of the complex molecules with all their activities by the supply of new material and the removal of the old and effete substances; whilst in death no renovation is possible, and the play of chemical affinities gradually reduces the several compounds to the simplest combinations of their elements. In the lower forms of life the structure is simple, and as there is no distinction of organs every part is capable of discharging a number of functions, each of which in the higher animal is limited to a special organ. The simplest forms of living beings with which we are acquainted are found in the class to which the term Protista is applied. In these the body is composed of a mass of protoplasm, through which granules are usually scattered, and the whole, or any part of it, can absorb nutriment from without, digest it, apply it to the nutrition of its own structure, cast out the indigestible matter, move from place to place, respond by movement to stimulation of various kinds, and undergo multiplication by division. In the higher animals each of these functions is limited to a definite organ. An alimentary canal is destined to digest the food, and prepare it for absorption into the circulating fluids. Definite vessels are formed, one segment being developed into a pulsating organ or heart, by which the fluids elaborated into blood are driven to all parts of the system, whilst special organs, as the bones, cartilages, muscles, and nerves, are subservient to movement, and to the reception, conduction, and the perception of impulses from without, and there are yet others which are subservient to reproduction.

General composition of the body.—The body is composed of certain ultimate elements united in part to form inorganic compounds, and in part

more complex organic compounds, chiefly made up of carbon and hydrogen either with oxygen alone, or with oxygen and nitrogen, named *proximate principles.* Some of these are in process of assimilation to the tissues and organs of the body, some form part of the organs themselves, and some are undergoing disintegration or decay, represent waste products, and are on their way to be discharged from the body.

The *ultimate elements* are carbon, hydrogen, oxygen, nitrogen, sulphur, phosphorus, chlorine, fluorine, potassium, sodium, calcium, magnesium, manganese, iron, and silicon. One or two of the elementary bodies are deserving of special notice by reason of their importance, and amongst these carbon, oxygen, nitrogen, phosphorus, and iron stand pre-eminent.

Carbon.—Carbon plays so important a part in the processes of plants and animals that the chemistry of the organic compounds has sometimes been termed the chemistry of the carbon compounds. The supply of carbon used by animals is in all instances originally derived from plants, which have the power of decomposing carbon dioxide under the influence of sunlight, of fixing the carbon, and of eliminating the oxygen. It is contained in large proportion in almost every article of food, fats, for example, containing more than half their weight of it, sugars and starches somewhat less than half, and meat in the uncooked state, including poultry and fish, about one-seventh of their weight of it. A man requires nearly 5,000 grains of it per diem. In its combustion or union with oxygen, for which gas it has a strong affinity, it gives off a large amount of heat. It unites with hydrogen in many proportions to form hydrocarbons, which are all volatile bodies, and present many examples of *isomerism*, that is, of cases where members of a family have the same composition, but present different physical or chemical properties.

Oxygen.—This gas is one of the most widely distributed substances in nature, and is essential to the existence of both plants and animals. It exists in the free state in the air, but, so far as is known, it is not liberated in that state by any agent, except by the green colouring matter of plants under the influence of sunlight. It forms a large proportion of the gases contained in water. A peculiar allotropic modification of it, named ozone, O_2O, is present in fresh air, but seems to be absent where much organic impurity exists. It is the only elementary body which directly participates in the vital processes of plants and animals, and it is essential to their maintenance. By its union with carbon and hydrogen it liberates the heat by which the temperature of the higher animals is maintained. About 7,000 grains are daily required.

Nitrogen.—It is noticeable that nitrogen, an element that has so few and such relatively feeble affinities, should enter into the composition of every living organism; yet it is perhaps to its presence that the extraordinary variety that characterises the functions, the unceasing change that is manifested in the tissues of plants and animals, is essentially due. Having no strong attraction, like that of oxygen for carbon, or of hydrogen for oxygen, it readily permits the decomposition and disintegration of the substances into whose composition it enters; and the elements with which it is combined (chiefly carbon and hydrogen) readily shift their position, and form sometimes more, sometimes less, complex molecules. Nitrogen enters into the composition of the most explosive compounds with which the chemist is acquainted, and many of the phenomena presented by nerve and muscle call to mind and have actually been likened to an explosion. Animals derive their nitrogen exclusively from plants. Plants obtain their supplies

of this element partly from ammonia and its salts, and partly from the nitrates, both of which are contained in the soil, and to a small amount in the air.

Iron.—This remarkable metal is uniformly present in the tissues, and especially in the blood of the higher animals. It is an essential constituent of hæmoglobin, and does not seem to be replaceable by any other element, not even by its nearest ally, manganese. Its presence appears to be associated with the power hæmoglobin possesses of combining with oxygen gas, and of readily yielding up this gas to substances which, like the tissues, have a stronger affinity for it. The body of an adult contains about 3 grammes, or 46 grains.

Phosphorus is only present in three of the organic constituents of the body: glycerin-phosphoric acid, lecithin, and nuclein. The proteids contain no phosphorus, but are difficult to free from lecithin and nuclein. In all three of the above-named bodies phosphorus is found in combination with oxygen in the proportion represented by the formula PO_4. Glycerin-phosphoric acid $C_3H_9PO_6$, as well as lecithin $C_{44}H_{90}NPO_9$, are simple ethers, and it is probable that nuclein is either an ether or an amide-like body, since it neither gives off phosphoric acid when acted upon by alkalies in the cold, nor is easily decomposed by hydrochloric acid.

The **inorganic compounds** are water and free hydrochloric acid; the carbonates, chlorides, fluorides, sulphates, and phosphates of the alkalies, and alkaline earths. The amount of *water* is 58·5 per cent. of the body weight, but different tissues contain very different proportions. Thus, the kidneys contain 82·7 per cent., the bones 22, the teeth 10, and the enamel only 0·2 per cent. The most important of the inorganic salts are sodium chloride, sodium phosphate, sodium carbonate, calcium carbonate and phosphate,

and potassium chloride. *Sodium chloride* is very widely distributed through the body, no tissue or fluid being destitute of it. It constitutes about four parts per 1,000 of the blood, and varies only to a small extent whether much or little is ingested with the food. The desire for it when, from any circumstance, the quantity supplied in the diet of the animal is insufficient, is imperious. Boussingault showed many years ago that when, of two sets of oxen, one was allowed the unrestricted use of salt, and the other was as far as possible deprived of its consumption, a marked contrast was observable between them, and manifestly to the advantage of the former, the fat being more abundant and the hide in better condition. Brücke mentions that many military deserters, who live a bandit life in the mountains of Salzburg and Carinthia, risk their liberty and even lives to obtain it in town or village. The tax or gabelle on salt is always a productive one. If salt be completely excluded from the food albumen soon appears in the urine. *Sodium carbonate* and *sodium phosphate* confer alkalinity upon the blood, thus aiding in the solution of its albumen, promoting its passage along the capillaries, and playing an important part in the absorption of gases, and consequently in the process of respiration.

The *gases* of the body are O, and perhaps ozone, H, N, CO_2, CH_4, NH_3, and H_2S.

The **proximate organic compounds** may be divided into two groups; the nitrogenous, and the non-nitrogenous.

The chief *nitrogenous* or *azotised compounds* are: Proteids, including the albumins, fibrin, casein, globulin, and peptones; the Albuminoids, mucin, chondrin, glutin, keratin, elastin, and ferments; the Biliary acids; Cerebrin, lecithin, and many others.

The principal *non-azotised compounds* are the Sugars: grape sugar, milk sugar, inosite, glycogen,

and cellulose; the Fats, stearin, palmitin, and olein; and the Organic Acids, formic, butyric, capronic, lactic, and sarcolactic acids.

The following synopsis of the chief proteid bodies is taken from Gamgee's "Physiological Chemistry," and should be carefully studied.

Soluble in pure water.

Class I.—**Albumins.**—Proteid bodies, which are soluble in water, and which are not precipitated by alkaline carbonates, by sodium chloride, or by very dilute acids. If dried at a temperature below 40° C. they become yellow and transparent, break with vitreous fracture, and are soluble in water; coagulation occurs between 65° C. and 73° C.

1. *Serum albumin.*— Specific rotation $(a)_D = -56°$, not precipitated from its solutions on the addition of ether.
2. *Egg albumin.* — Specific rotation $(a)_D = -35{\cdot}5°$, precipitated from its solution on agitation with ether.

Class II.—**Peptones.**—Proteid bodies, exceedingly soluble in water; solutions not coagulated by heat; nor precipitated by sodium chloride, nor by acids or alkalies. Precipitated by a large excess of absolute alcohol, and by tannic acid. In the presence of much caustic potash, or soda, a trace of solution of copper sulphate produces a beautiful rose colour.

Insoluble in pure water, but soluble in weak solutions of common salt.

Class III.—**Globulins.**—Proteid substances, which are insoluble in pure water, but soluble in dilute solutions of NaCl. Their solutions are coagulated by heat; they are soluble in very dilute hydrochloric acid, being converted into acid-albumin. They are also readily converted by alkalies into alkali-albumins.

1. *Vitellin.*—Not precipitated from its solution when these are saturated with common salt.
2. *Myosin.*—Precipitated from its solution in weak common salt when these are saturated with sodium chloride. Solutions coagulate at 55° to 60° C. Solutions in common salt not coagulated by solution of fibrin ferment.
3. *Fibrinogen.*—Soluble in weak solutions of NaCl. Precipitated from them completely on the addition of NaCl, when this amounts to 12 or 16 per cent. Solutions coagulate on the

addition of fibrin ferment. Temperature of coagulation 56° C.

4. *Paraglobulin.*—Soluble in weak solution of sodium chloride. From weak alkaline solutions paraglobulin is precipitated by the addition of a very small quantity of NaCl. A further addition of this body effects resolution of the precipitate, which is thrown down again, though still not completely, when the amount of NaCl in solution exceeds 20 per cent. Paraglobulin is completely precipitated when its solutions are saturated with magnesium sulphate. Its solutions are not precipitated by addition of fibrin ferment. Temperature of coagulation varies, according to the amount of salts present, and mode of heating, between 68° C. and 80° C.

Insoluble in pure water, but soluble in weak solutions of common salt.

Class IV.—**Derived albumins.**—Proteid bodies, insoluble in pure water, and in solutions of NaCl, but readily soluble in dilute HCl, and in dilute alkaline solutions. Solutions not coagulated by heat.

1. *Acid albumins.*—Obtained by the action of dilute acids, especially HCl, upon solutions of proteids, by action of strong acids upon solid proteids, and as first products in the action of gastric juice upon proteids. On neutralising solutions of acid albumins they are precipitated even in the presence of alkaline phosphates. NaCl added to saturation also precipitates them.

2. (*α*) *Alkali albumins.*—Obtained by the action of dilute alkalies upon the proteids. Possess the properties of sub-class 1, with the exception that in the presence of alkaline phosphate, the solutions are not precipitated by neutralisation; when heated with strong solution of caustic potash, potassium sulphide is not formed.

(*β*) *Casein.*—The chief proteid constituent of milk. Same properties as *α*, but when treated with strong solution of caustic potash, potassium sulphide is formed. In milk is coagulated by rennet.

Class V.—**Fibrin.**—Insoluble in water, and in weak solution of NaCl. White, elastic, solid, usually exhibiting fibrillation under the microscope; swells up in cold hydrochloric acid of ·1 per cent., but does not dissolve. When thus swollen, dissolves with ease when a solution of pepsin is poured over it. When heated for a great many hours at

40° C. in dilute HCl it dissolves, and the solution contains acid-albumin.

CLASS VI.—**Coagulated proteids.**—Insoluble in water, dilute acids, and alkalies. Gives Millon's reaction. Are dissolved when digested at 35° C. to 40° C. in artificial gastric or pancreatic juice, giving rise to peptones.

CLASS VII.—**Lardacein** or **amyloid substance.**—Insoluble in water, in dilute acids, in alkaline carbonates; not dissolved by gastric juice at the temperature of the body, coloured brownish-red or violet by iodine.

General characters of the proteids.—All the compounds included in this group of substances contain nitrogen and sulphur, and their chemical composition is expressed by a formula more or less closely resembling the following: $C_{54}H_7N_{16}O_{22}S_4$. They are amorphous, with variable solubility in water and acids; usually soluble in alkalies; almost insoluble in alcohol and ether. The aqueous solutions are neutral. They are not volatile; they burn with an odour of burnt feathers, giving off ammoniacal fumes, and leaving a residue of ash which chiefly consists of lime phosphate. Exposed to the air they easily undergo decomposition. Calcined with potash, or boiled with sulphuric acid, they yield leucin and tyrosin. Hot concentrated nitric acid converts them into a yellow body, xanthoproteic acid. Treated with acids or with alkalies, or when allowed to undergo putrefactive decomposition, they give, amongst others, the following products of decomposition: volatile fatty acids; oxalic, acetic, formic valerianic, fumaric, and asparagic acids; leucin, tyrosin, and ammonia. When treated with oxydising agents, they yield formic, acetic, propionic, butyric, valerianic, capric, and benzoic acids; the aldehydes of these acids and volatile organic bases, aceto-nitril, valero-nitril, and propio-nitril. They rotate polarised light to the left. They are precipitated from their solutions by an excess of the strong mineral acids, by acetic or hydrochloric acid, and potassium ferrocyanide, the basic acetate of lead, mercury bichloride, tannin, and by potash carbonate in powder.

Tests for the proteids.

1. *Nitric acid test.*—Heat the liquid, and add nitric acid till the reaction is strongly acid: a precipitate falls which undergoes no change on the addition of acid.
2. *Sodium sulphate test.*—Add acetic acid till the reaction is strongly acid. Mix with an equal volume of concentrated solution of sodium sulphate, and boil; the proteids are precipitated.

3. *Pietrowski's test.*—Warm the liquid containing albumin with a moderate quantity of solution of potash or soda, and then add one or two drops of copper sulphate; the liquid assumes a violet colour.
4. *Xanthoproteic reaction.* — Heat with concentrated nitric acid; the liquid, if it contain a proteid, will assume a yellow tint, which becomes reddish-orange by the action of alkalies.
5. *Millon's test.*—Millon's reagent is made by dissolving in the cold one part of mercury in its weight of concentrated nitric acid; the solution is completed by applying gentle warmth. Two volumes of distilled water are then added, and the fluid decanted. This test gives a red colour with liquids containing proteids, which is more marked when they are heated to 60° C. or 70° C.
6. *Adamkiewicz's test.*—Every proteid, when dissolved in an excess of glacial acetic acid, gives, on the addition of concentrated sulphuric acid, a beautiful violet colour and a slight fluorescence (Beaunis).

Carbohydrates. These include:

1. *Starch* $C_6H_{10}O_5$, formed in and produced by plants growing under the influence of light. It is often stored up as aliment in tubers and fruit, and consists of granules presenting concentric markings. It is insoluble in cold, but swells and becomes gelatinous in hot water, which dissolves the *granulose*, but leaves undissolved the *cellulose* of the starch granules. Gives a blue colour with free iodine. Exposed to heat the blue tint vanishes, but will return if the liquid be suddenly cooled. Starch, on being heated to 210° C., is converted into *dextrin*, which also appears in germinating seeds. When starch paste is boiled with dilute acid it is converted through some intermediate stages into dextrin and then into sugar, and the same conversion is effected by the saliva, pancreatic and intestinal juices.
2. *Sugars.*—These are substances having a more or less sweet taste, usually soluble in water, and destroyed by strong sulphuric acid, which abstracts the water of these compounds and leaves only the carbon. The most important are glycose $C_6H_{12}O_6$, lactose $C_{12}H_{24}O_{12}$, saccharose $C_{12}H_{22}O_{11}$, and glycogen $C_6H_{10}O_5$. On fermentation they yield CO_2 and alcohol. The tests for glycose are:
 1. *Trommer's test*, which depends on the circumstance that sugar in an alkaline solution acts as a reducing agent. To the saccharine fluid about one-fourth of its bulk of soda or potash lye is added, and a dilute solution of copper sulphat-

A slight clouding occurs from precipitation of hydrate of copper oxide, which dissolves on shaking. On heating the fluid, if sugar be present, a yellowish precipitate of cuprous oxide takes place.

2. *Bottcher's test.*—An alkaline solution of bismuth is reduced by sugar to bismuth suboxide, the oxide being precipitated as an olive green and ultimately black powder.
3. *Moore's test.*—The fluid is boiled with caustic alkali, and becomes, if sugar be present, first yellow, then brown, and then blackish. On the addition of nitric acid a smell of caramel is perceptible.
4. *Mulder and Neubauer's test* consists in the addition of a sufficient quantity of a solution of indigo carmine to give the saccharine solution a faint blue tint, and applying sodium carbonate; on applying heat the colour changes to green, purple, and red. On agitation with air the fluid recovers its blue tint.
5. *Runge's test.*—Saccharine solutions, when evaporated to dryness with sulphuric or hydrochloric acid in a water bath in a porcelain capsule, leave behind a black shining residue.
6. *Silver test.*—Diluted solution of grape sugar, on being boiled with silver nitrate and ammonia, leaves a metallic deposit on the surface of the vessel. Alcoholic solution of grape sugar, mingled with alcoholic solution of caustic alkali, causes a precipitation of a compound of alkali and sugar in the form of white flocculi.

Fats.—The fats are ethers derived from the triatomic alcohol glycerin $C_3H_5(OH)_3$. They are widely distributed both in plants and in animals. They contain very little oxygen. They are soluble in ether, benzol, chloroform, and in boiling alcohol. Dropped on paper they give a characteristic grease spot. Shaken up with colloid substances they give an emulsion. Heated with water above steam heat, or exposed to the action of certain animal ferments, as that of the pancreas, they take up water and split into glycerin and free fatty acids. When these essential fats are boiled with solutions of the alkaline hydrates or carbonates, they undergo the process of saponification, decomposing as before into glycerin, and the fatty acids, but the latter immediately combine with the alkaline metal to form a soap, which is, in fact, a

soluble salt. The three principal fats of the human body are tristearin, tripalmitin, and triolein. The following formulæ represent, according to Gamgee, the composition of these bodies:

Glycerin $C_3H_5(OH)_3$ { Palmitin, $C_3H_5(OC_{16}H_{31}O)_3$; Stearin, $C_3H_5(OC_{18}H_{35}O)_3$; Olein, $C_3H_5(OC_{18}H_{33}O)_3$

Palmitic acid, $C_{16}H_{31}O,OH$

Stearic acid, $C_{18}H_{35}O,OH$

Oleic acid, $C_{18}H_{33}O,OH$.

Stearin melts at about 60° C., palmitin at about 45° C., olein at about 30° C. Stellate crystals of stearin and palmitin often occur in fat cells.

Ferments and fermentation.—The phenomena of fermentation are so remarkable that they have at all times attracted attention. From a remote period of antiquity, and in every nation that has emerged from barbarism, it has been recognised that the heavy and indigestible mass resulting from the mixture of flour with water can be rendered light and spongy by the admixture of a small quantity of yeast, and that, after baking, the now porous mass is converted into wholesome and digestible bread. In like manner, the addition of a small quantity of a substance resembling yeast to any saccharine fluid changes its nature, renders it creamy with minute bubbles, and after a time ends by leaving the body of the fluid clear and transparent, with a sediment at the bottom and a scum at the top, but now converted into an alcoholic fluid, variously named beer or wine, mead or pulque, but always with intoxicating properties, and a flavour dependent on the source from which the sugar was originally derived. The singular features of the process are the minute quantity of the exciting agent that is required—"a little leaven leaveneth the whole lump"—the rapidity and certainty with which at ordinary temperatures the action takes place, and the constancy of the result. In all cases the sugar originally present is broken up into alcohol and carbon

dioxide, though there are certain by-products which prove that the action is complex. Pasteur's experiments have shown that 100 parts of cane sugar, in fermenting, first become converted into 105·4 parts of glucose, which then break up, yielding (approximately) of alcohol 51·1 parts, of carbon dioxide 49·4, succinic acid 0·7, glycerine 3·2 parts, matter passing to the yeast 1 part, and traces of the higher alcohols, such as fusel oil and the compound ethers. Omitting the by-products, the decomposition may be thus broadly formulated :

$$\underset{\text{Glucose.}}{C_6H_{12}O_6} = \underset{\text{Alcohol.}}{C_2H_6O} + \underset{\text{Carbon dioxide.}}{2CO_2}.$$

The range of temperature most favourable to the process of fermentation is from 20° to 24° C. (68° to 75° F.). Heat is liberated during the process, about 83 heat-units being evolved for each unit weight of sugar destroyed. Fermentation can be arrested by the addition of small quantities of certain reagents named antiseptics, examples of which are found in corrosive sublimate, sulphurous acid, boracic acid, thymol, and carbolic acid.

Ferments have been separated into two groups, the "formed" and the "unformed" or "soluble" ferments. In the case of the alcoholic fermentation, the exciting agent of the process appears to be a unicellular alga named *saccharomyces*, the various forms of which act with different degrees of activity in different fluids. The cells, which are sometimes separate, sometimes arranged in chains, multiply by gemmation or budding, and are about $\frac{1}{100}$ mm. in diameter. The ferment of wine and beer is therefore a "formed" ferment, and the breaking up of the molecule of sugar is regarded by many as a physiological function of the cell ; but it is only right to add that sweet fruit, kept in an inert atmosphere, devoid

of free oxygen, evolves carbonic acid with formation of alcohol, and it has been proved by Pasteur that this fermentation is not accompanied by the development of any microscopic organism. Closely related to this is the well-established fact that large quantities of sugar may be made to ferment by means of yeast, without the latter multiplying to any noteworthy extent. On the other hand, the makers of German barm obtain large quantities of yeast without producing much alcohol. Brefeld, indeed, succeeded, by means of a peculiar artifice, in growing saccharomyces in brewers' wort without producing a trace of alcohol (Dittman). Hence it would appear that vinous fermentation, far from being the characteristic life function of healthy saccharomyces, is dependent on a certain pathological condition of cells, normally growing in darkness, which is brought about by immersing them in saccharine fluids, and shutting them out from oxygen, which they need for their healthy development; and the best authorities go no farther than to admit that these living organisms are the only known sources for the ferments proper, which in themselves are chemical substances pure and simple. Many other kinds of fermentation, such as that, for instance, in which

hydrated milk sugar		lactic acid,
$C_{12}.H_{22}O_{11}.H_2O$	yields	$4C_3H_6O_3$,

are associated with the multiplication and development of a "formed ferment," which in this case is known as the *bacterium lactis*, and is of extremely small size. Similar organisms are found in viscous fermentation, to which wine is liable when it becomes ropy and contains a kind of gum; in butyric fermentation, where glucose breaks up into lactic acid, butyric acid, carbon dioxide, and hydrogen gas; and in putrefaction, which is a highly complex process.

The cases of fermentation in which the ferment is "soluble," and the action a purely chemical one, are numerous, and have a special interest for the biologist, since they include some of the most important metabolic processes in the body, such, for example, as the action of ptyaline and amylopsin upon the starches, of pepsin and trypsin on the proteids, and of steapsin on the fats. These ferments appear to be generated in the cells of the several organs by which they are excreted, and as a rule they are destroyed when in the moist state by exposure to a temperature at or near that of boiling water. Other examples of soluble or unformed ferments are presented by the action of mineral acids upon cane sugar, by which it is "inverted," or converted, with absorption of water, into dextrose and levulose; the conversion of starch by the same agents into dextrine and dextrose; the disintegration of salicine into glucose and saligenin by muriatic acid; the action of diastase upon starch, which it converts into dextrine and dextrose; and lastly, the action of emulsine upon amygdaline. In all these cases there is a conversion of anhydrides into hydrates.

CHAPTER II.

THE BLOOD.

Blood may be regarded as a tissue in which the matrix is fluid and in which cell-like elements float, the whole being in constant motion.

Physical properties of the blood.—Blood is of a red colour, varying in different parts of the circulating system from a carmine or almost purple tint to vermillion. It is usually brighter in the arteries than in the veins, owing to the arterial blood being charged with oxygen, whilst that in the veins

contains deoxydised hæmoglobin. Arterial blood is monochroic, venous is dichroic; that is to say, that when seen by reflected light it is red, but when by transmitted light, bottle-green. The blood both of arteries and of veins varies under different circumstances. Thus, in women in an advanced stage of pregnancy, the arterial blood is somewhat darker than at other periods, since it is charged with the carbonic acid of the fœtus as well as its own. On the other hand, it is paler in splenic diseases, in chlorosis, and leukæmia. The blood of different veins is not equally dark; the brightest blood is that returning from the kidneys, and from secreting glands in action. Blood is exceedingly opaque, a comparatively thin layer entirely intercepting the passage of light. It presents an alkaline reaction when freshly drawn, which, however, soon becomes less marked, owing to the formation of acids. The reaction may be shown by impregnating neutral porous plates with red tincture of litmus. On allowing a drop of blood to fall upon the part, the corpuscles rest on the surface, whilst the fluid parts of the blood are absorbed, and effect a change of colour in the plate a little below the surface. The smell of blood resembles that of the animal from which it is drawn, and may be rendered more perceptible by the addition of a little strong sulphuric acid, which expels the volatile fatty acids to which it is due. The taste is saline and mawkish. Its sp. gr. is 1056, with extremes of 1045 and 1077.

The **spectrum of the blood.**—When blood is diluted with water, so that it contains 7·4 per cent. of dry colouring matter, a layer 1 centimetre thick transmits no light; but when it is reduced to 7 per cent. a faint narrow line of light is visible at C. In proportion as the blood is further diluted, more and more rays are transmitted, till at length only *two absorption bands* remain, which lie between D and E (Fig. 1, I).

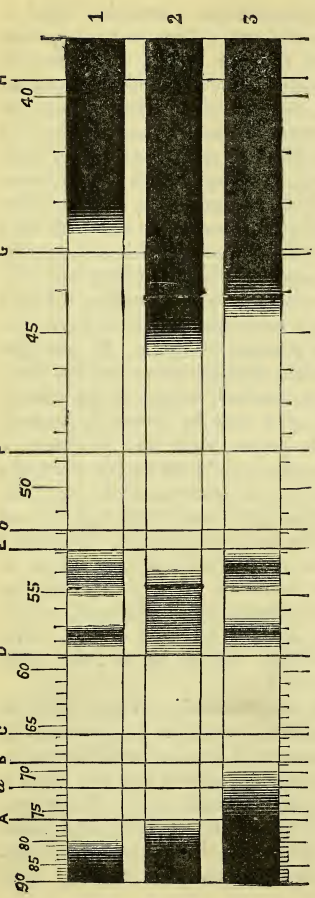


Fig. 1.—Spectrum of the Blood.

This is the absorption spectrum of arterial blood, or of *oxyhæmoglobin*.

The two bands are most distinctly seen when a stratum 1 centimetre thick of a solution containing one part of hæmoglobin in 1,000 is examined.

The absorption band at D is still visible in a layer 1 centimetre thick of blood diluted with 4,500 parts of water. But when diluted beyond this degree, no absorption band can be perceived.

The darker red of venous blood is due to the circumstance that it both transmits and reflects chiefly the darker rays of the spectrum between A and C of Frauenhöfer's lines. Arterial blood both transmits and

reflects the brighter rays between C and D. It absorbs the green rays. Venous blood transmits green and blue in part; and hence its bluish appearance in thick layers, and its greenish tint in thin layers. The difference between the hue of arterial and venous blood is but slight; both have a cherry-red colour.

If, by means of reducing agents, the oxygen be withdrawn from the blood, the oxyhæmoglobin ordinarily present is reduced or converted into hæmoglobin, the double absorption band disappears and is replaced by a single band (Fig. 1, 2), which occupies a position nearly intermediate to the two bands of oxyhæmoglobin. Such a reducing agent is found in the light green fluid which results from the addition of ammonia in excess to a solution of ferrous sulphate and tartaric acid. When a few drops of this solution are added to blood oxydised by exposure to air, the colour of the blood becomes darker, and the double band of oxyhæmoglobin is replaced by a single band of reduced or ordinary hæmoglobin. The simple act of shaking the vessel, by exposing the colouring matter to oxygen, causes the double band to reappear to be again changed into the single band by repose. It is thus evident that reduced hæmoglobin has a stronger affinity for oxygen than the ferrous salt, but yields it to the salt after a short period. Ordinary hæmoglobin can also be obtained from oxyhæmoglobin by exposing the blood or solution of hæmoglobin to the low pressure of a Torricellian vacuum, the oxygen separating from the hæmoglobin by what is termed the act of dissociation. Gamgee found that at 40° C. the dissociation occurred at a pressure of about 30 mm. of mercury. It is remarkable that in blood which has been exposed to the action of carbonic oxide gas, the spectrum presents two absorption bands which are almost, though not quite, identical with those of oxyhæmoglobin (Fig. 1, 3), the second band, or that

nearest to the E line of the solar spectrum, being shifted a little towards the violet end of the spectrum. The affinity of CO for hæmoglobin is stronger than that of oxygen for hæmoglobin, and hence when the blood and carbonic oxide come into contact the oxygen is displaced, and, as the tissues are incapable of either combining with or reducing the CO, the deficiency of oxygen soon makes itself felt, and symptoms of poisoning are produced.

Quantity of the blood.—The quantity of the blood in man is estimated to be from one-twelfth to one-fourteenth of the weight of the body, so that a man weighing twelve stone has about fifteen pounds of blood in his body. It may be determined by Welcker's method, which consists in collecting all the blood that can be obtained by opening the larger vessels. This gives approximately the total quantity contained in the body, but approximately only, for a considerable quantity still remains in the capillaries of the muscles, and of various isolated organs, as the brain, spleen, and liver. To estimate this extra quantity the body is finely minced and thrown into a large quantity of water. The colour of the infusion is then compared with that of a series of test liquids in which water is mingled with known quantities of blood, and a tolerably accurate conclusion may thus be drawn of the quantity present in the body after the general bleeding. A modification of this method has been employed by Gescheidlen, in which the tint of the blood is rendered uniform, and decomposition retarded by treating the blood with carbon monoxide. Lehmann, with Weber, obtained a higher number than that above given. These observers determined the weight of two criminals before and after decapitation, and having washed out the vessels with water, the quantity of blood remaining in the body was calculated by instituting a comparison between the

solid residue of the pale red aqueous fluid and that of the blood which first escaped. By way of illustration the following gives the results of one of the experiments with which the other was in close accordance. The living body of one of the criminals weighed 60140 grammes, and after decapitation the same body weighed 54600 grammes, consequently 5540 grammes of blood had escaped; 28·560 grammes of the blood yielded 5·36 grammes of solid residue; 60·5 grammes of sanguineous water collected after the injection contained 3·724 grammes of solids; 6050 grammes of the sanguineous water that returned from the veins were collected, and these contained 37·24 grammes of solids, which corresponds to 1980 grammes of blood; consequently the body contained 7520 grammes of blood (5540 escaping in the act of decapitation and 1980 remaining in the body), hence the weight of the whole blood was to that of the body nearly in the ratio of one to eight. The quantity of blood is greatly increased after a meal, especially when liquid has been taken. It does not diminish but rather increases relatively to the weight of the body in inanition. In the new-born child it is only about one-nineteenth of the total weight of the body. An increase takes place during pregnancy, especially in the latter half. In plethora the quantity of the blood is augmented, in anæmia diminished. After severe hæmorrhages the loss of blood is soon restored, though the corpuscles are manifestly fewer in number.

Morphological or formed elements of the blood.—Blood contains coloured and colourless corpuscles, the physical characteristics of which are fully detailed in the companion volume, "The Elements of Histology." The *coloured corpuscles* are elastic and have a specific gravity of about 1088. Their elasticity is shown by the temporary alteration in form they undergo in bending round an angle of division of

a blood-vessel. The essential purpose they fulfil is that of oxygen-carriers; for the hæmoglobin they contain combines with oxygen during their transit through the lungs, and surrenders it to the tissues as it traverses them. The number of the red corpuscles is enormous; a cubic millimetre contains between 4,000,000 and 5,000,000, and it may be estimated by diluting a definite quantity of blood with many times its bulk of water, distributing the mixture evenly over a stage ruled into squares of known size, and then counting the number of corpuscles in each square. Estimates which are, of course, only approximate show that the red corpuscles of an adult present an aggregate surface of about 3,000 square yards, whilst the surface they present for the absorption of oxygen in the lungs each second is about 80 square yards.

The *white corpuscles* are small nucleated masses of protoplasm, capable of executing amœboid movements at the rate of progression of 13 millimeters per minute, and much fewer in number than the red, the number in 1 cubic millimetre of blood varying from 4—7,000.

The protoplasm of the colourless corpuscles is a proteid which undergoes partial decomposition, or at least coagulation at 40° C. It swells and becomes transparent when treated with acetic acid. It dissolves in a 10 per cent. solution of NaCl, the nuclei, which consist of nuclein, remaining undissolved. The white corpuscles contain glycogen, recognisable by the reddish colour it gives with potassium iodide and iodine. They sometimes contain a few minute fat granules.

The use of the colourless corpuscles is not certainly known, but amongst other purposes they probably subserve the repair of tissues and aid in the production of the coloured corpuscles. They contain myosin, fat particles, cholesterin and protagon, nuclein and glycogen.

Other colourless corpuscles have been described by

Norris, which have been shown by Mrs. Hart to be red corpuscles from which the colouring matter has been dissolved out.

Coagulation of the blood.—Blood, on being withdrawn from a vessel, is perfectly fluid, but, within a few minutes, it first becomes viscous, and then sets or coagulates, becoming converted into a solid gelatinous mass, and giving off at the same time a peculiar odour termed the *halitus*. Small transparent beads soon appear on the surface, and, running together, form a layer of yellowish fluid. The fluid is the *serum;* the red solid mass from which the serum exudes is the *clot*. The time that elapses between the escape of blood from a vessel and the occurrence of coagulation varies. The minute drops that spirt from a divided artery, and fall on a rough surface, like baize, during an operation, often coagulate in a minute, or, at most, within two minutes; but, when drawn in mass into a bowl, coagulation does not commence for ten minutes, though the blood gradually becomes thicker. In the horse under ordinary conditions, and in other animals if the blood be rapidly cooled, a triple separation of its constituents may be observed. The red blood-corpuscles, being the heaviest, sink to the bottom of the vessel; lying upon them is a thin layer of white corpuscles, whilst the upper part of the fluid column consists of nearly pure liquor sanguinis. Notwithstanding this separation of parts, the column coagulates with nearly equal firmness throughout, and the exudation of serum takes place in the customary manner. It is possible to filter blood, and the corpuscles are found to remain on the filter, whilst the liquor sanguinis passes through it. In this case the liquor sanguinis will set as usual, showing that the presence of the corpuscles is not essential to the act. Under the microscope, it may be seen that, just before coagulation sets in, the red

corpuscles have a tendency to adhere by their flat surfaces, so as to resemble small piles of coin.

Circumstances affecting the rapidity of coagulation. — Cold approximating the freezing point of water retards coagulation, and, if the cooling be rapidly effected, the blood may even be frozen before it has had time to coagulate. In this condition it may be kept for an indefinite period, but, if thawed, it quickly sets. Coagulation may be prevented by the addition of large quantities of various neutral salts, such, for example, as sodium potassium or magnesium sulphate or chloride, the alkaline carbonates and nitrate of potash, by syrup, pepsin, and white of egg, and by acetic acid added in sufficient quantity to give it an acid reaction. Venous blood coagulates more slowly than arterial, apparently in consequence of the larger proportion of carbonic acid gas it contains. Hence, too, coagulation is slow in the blood of those who have been asphyxiated. Coagulation of normal blood never takes place as long as it is moving within the vessels; and, even if it be confined to a limited portion of an artery or vein by pressure applied at two points without injury to the vascular walls, it still exhibits little or no tendency to coagulate. If, however, the wall of the vessel be injured, as usually occurs when ligatures are cast around it and tied, the contained blood sets readily enough. Blood rapidly drawn from the body into a smooth vessel, such as glass or china, sets slowly. Under all these circumstances, the corpuscles have time to settle towards the bottom of the vessel, leaving the plasma at the upper part clear. The coagulation of this clear layer of plasma forms the *buffy coat* seen in the slowly coagulating blood of the horse, and in inflammatory affections in man.

Coagulation is hastened by free exposure of the blood to air, and it occurs quickly in blood flowing from a small vein or from a small orifice in a vein,

especially when it falls on a rough surface or is received in a metallic vessel which presents many points at which the process may commence. It is hastened by a moderately high temperature. If exposed to a temperature approaching 150° Fahr., coagulation of the serum albumin takes place.

During coagulation the blood becomes less alkaline, the oxygen it contains diminishes, the carbon dioxide increases, and a slight rise of temperature occurs.

Cause of the coagulation of the blood.—The coagulation of the blood is due to the solidification of fibrin, a proteid believed to be formed by the union, under the influence of a *ferment* and in presence of small quantities of neutral salts and alkalies, of two compounds originally existing in solution named *fibrinogen* and *paraglobulin*. The ferment, which is allied to the proteid, does not pre-exist in the blood, but develops after the blood is withdrawn from the vessels, unless, as Wooldridge maintains, the active agent is lecithin, and in either case it appears to be derived from the breaking down of the colourless corpuscles; and these corpuscles also yield a part, and perhaps a large part, of the paraglobulin. Fibrin can be obtained in a tolerably pure state by whipping blood with a bundle of twigs before coagulation has commenced. It then appears as a buff-coloured, stringy substance, which has considerable elasticity. Normal blood contains less than 0·1 per cent. of fibrin. For the chemical characters of fibrin, *see* page 9.

It is remarkable that the serous fluids poured forth in inflammatory affections of the pleura, pericardium, peritoneum, tunica vaginalis, and other serous membranes, exhibit little or no tendency to coagulate; but, if a little blood from which the fibrin has been removed by whipping be added to either of them, coagulation at once occurs. The whipped, or defibrinated, blood appears to contain something

capable of inducing coagulation when brought into contact with another substance contained in the transudate; and Schmidt believes he has been able to show that whilst the ferment, and a large part of the paraglobulin, proceed from the white corpuscles, the fibrinogenous substance is contained in solution in the liquid, and that he has isolated these substances.

The reasons for believing that the *ferment* is derived from the white corpuscles are :

(1) That there is evidence that the ferment does not proceed from the red corpuscles.

(2) That blood freed from its white corpuscles by filtration at 0° C. coagulates late and slowly; yet, if temporarily raised to 10°—20° C., and re-cooled and filtered, the filtrate, though destitute of white corpuscles, is rich in ferment, the corpuscles having had the opportunity of parting with it.

(3) That the quantity of ferment in filtered plasma, which removes the white corpuscles, is not greater at the end of coagulation than at the beginning, whilst, in non-filtered plasma, the ferment undergoes great increase during the act of coagulation.

The reasons for believing that the paraglobulin is partly derived from the white corpuscles are :

(1) That filtered plasma gives nearly 30 per cent. less fibrin than unfiltered plasma.

(2) That the number of white corpuscles in the blood is greater before than after coagulation.*

* A somewhat different view of the cause of the coagulation of the blood has lately been advanced by Olof Hammarsten, who maintains that paraglobulin, though it may exert a favourable influence, is not essential to the solidification of fibrin. He considers that all that is necessary for this purpose is a solution of fibrinogen and a ferment, for he finds that if the whole of the globulin is precipitated from serum by magnesium sulphate, coagulation will still occur, whilst if to a perfectly pure solution of fibrinogen a solution of ferment be added, coagulation at once takes place, the quantity of fibrin formed being always less than that of the fibrinogen originally present, which is due to the fibrinogen breaking up into fibrin, and a soluble globulin.

Bizzozero so far differs from Schmidt's views that he believes certain granular masses and plates found in the blood are the active agents, instead of the white corpuscles. Wooldridge refers coagulation to the presence of lecithin.

COMPOSITION OF THE BLOOD.

The quantitative composition of the blood varies considerably in different persons, and even in different parts of the same person. The following table represents that of the horse, but may be taken as similar to that of man :

1,000 parts of blood contain

- Cells, 328
 - Water 200
 - Solids, 128
 - Hæmoglobin 116
 - Other organic compounds 10
 - Salts 2
- Plasma, 672
 - Water 604
 - Solids, 68
 - Fibrin 7
 - Albumin 52
 - Fat 1
 - Other organic compounds 3
 - Potassium and sodium salts 4
 - Calcium and magnesium salts 1

The **proteids of the blood.**—The coloured corpuscles contain from 5 to 12 per cent. of proteids. The most important of these is hæmoglobin.

Hæmoglobin.—This substance stands almost alone in the complexity of its constitution, the formula for each molecule being $C_{600}H_{960}N_{154}FeS_3O_{179}$. It has a strong affinity for oxygen, 1 gramme of hæmoglobin being capable of taking up 1·27 cubic centimetres of oxygen at 0° C., and 1 metre pressure. It is then termed *oxyhæmoglobin*. The oxygen can be displaced by the air pump and various agents, and more

particularly by the tissues of the body, which have a stronger affinity for oxygen than hæmoglobin. It is then termed *reduced hæmoglobin.* Hæmoglobin therefore acts as an oxygen carrier, absorbing and combining with oxygen as it traverses the lungs, parting with it as it courses through the body. Oxyhæmoglobin crystallises in the forms shown in Klein's "Histology," p. 13. The crystals are doubly refracting and pleochromatic. They may be obtained by various methods, the principle in all of which is to effect the solution of the hæmoglobin, either in serum or water, and then by the addition of alcohol or by the agency of cold, or of both conjointly, to cause the hæmoglobin to crystallise out (Gamgee). Crystals of oxyhæmoglobin can easily be obtained from the blood of the guinea-pig, rat, dog, horse, and carp; with difficulty from the blood of man, the sheep, and rabbit; and with great difficulty from the ox, pig, and frog. Moist hæmoglobin is a pasty red mass, evincing when pure and when kept in vacuo little or no tendency to decomposition, readily dissolving in weak solutions of the caustic, and of the carbonated alkalies, and easily decomposed by strong alkaline solutions, as well as by acids and acid salts with formation of hæmatin. 100 grammes of blood contain 12 to 15 grammes of hæmoglobin. Hæmoglobin is the only substance in the blood which contains iron. There are 4·3 parts of iron in every 1000 parts of hæmoglobin.

Products of the decomposition of hæmoglobin.—When hæmoglobin undergoes decomposition without access of oxygen, it yields a proteid and a body named *hæmochromogen*, but when it is exposed to air for some time hæmoglobin loses its blood-red colour, assumes a brownish tint, presents an acid reaction, is precipitated by solutions of basic lead acetate, and gives a spectrum in which the two bands of oxyhæmoglobin are faint, whilst a new band

appears in the red near C. On adding some reducing agent, as sulphide of ammonium, the fluid gives the spectrum of reduced hæmoglobin, whilst on shaking the solution containing the latter with air, oxyhæmoglobin is again formed. These characters appear to be possessed by hæmoglobin whilst in process of translation into hæmatin and a proteid, and to this intermediate stage the term *methæmoglobin* has been applied. Spots of blood dried in the air contain only methæmoglobin.

Hæmatin.—This is one of the products of the decomposition of hæmoglobin by the action of acids or of alkalies, in presence of oxygen. It is also formed by the oxydation of hæmochromogen, and reducing agents convert it again into hæmochromogen. When blood is treated with acetic acid it assumes a brown tint, and the acid hæmatin formed can be dissolved out with ether. Pure hæmatin is of blue-black colour with metallic lustre, and does not crystallise. Its formula is $C_{68}H_{70}N_8Fe_2O_{10}$. It contains 12·6 per cent. of oxide of iron. It is insoluble in water. The etherial solution presents four absorption bands, two between C and D, one between D and E, and another between *b* and F.

Hæmin.—When a drop of blood is boiled with acetic acid and a little common salt, it immediately becomes brown, and on evaporation reddish-brown. Prismatic crystals may be obtained, which are those of hæmin. They are insoluble in water, scarcely soluble in hot alcohol and ether, soluble in liquor potassæ. They are of much importance in medico-legal enquiries.

Hæmatoidin.—This name is given to the yellow microscopical crystals found in old apoplectic clots and other extravasations of blood. They appear to be identical in form with those of bilirubin, and when treated with fuming nitric acid give the same colour

reaction as the chief colouring matter of human bile (Gamgee). They contain no iron.

PLASMA OF THE BLOOD.

The fluid in which the corpuscles float is the plasma. It is viscous, of yellowish colour when in mass, with specific gravity of 1026 to 1029. Its reaction is alkaline. It is capable of coagulation in the presence of white corpuscles, or of the products of their disintegration. It contains certain proteids, the most important being

Paraglobulin.—This is also known under the names of serum globulin and of Schmidt's fibrinoplastic substance. It is obtained by diluting plasma with 10 to 15 times its volume of ice-cold water, and transmitting through the fluid a stream of carbon dioxide. It may also be obtained by adding 4 drops of a 25 per cent. solution of acetic acid to 10 cubic centimetres of serum, diluted with 150 cubic centimetres of H_2O, and, still better, by adding magnesium sulphate to complete saturation, when the whole of the paraglobulin falls. It is probably in part contained in solution in the plasma, and in part in the colourless corpuscles. It coagulates at about 75° C.

Fibrinogen.—After the paraglobulin has been removed from plasma, if the fluid be still further diluted and CO_2 passed, fibrinogen is precipitated. This substance is insoluble in pure water, but soluble in water which holds oxygen in solution. Like paraglobulin, it is soluble in a solution of sodium chloride, containing 5 to 8 per cent. of the salt. When the quantity of salt attains 12 to 16 per cent., fibrinogen is precipitated, whilst paraglobulin remains in solution. Solutions of fibrinogen coagulate at 56° C. 100 grammes of the plasma of a horse have been found in one experiment to contain 0·4299 gramme of fibrinogen, and to yield 0·375 gramme of fibrin.

The nature of fibrinogen has been very carefully investigated by Hammarsten, who obtains the substance to which he applies this name by opening a vein in the horse and receiving three or four volumes of blood in a vessel containing one volume of a saturated solution of magnesium sulphate, stirring the mixture vigorously and filtering. The corpuscles are thus separated from the fluid consisting of plasma and saline solution. Saturated solution of common salt is now added, and the precipitate collected in a filter; this is now extracted with an 8 per cent. solution of common salt, then precipitated with a saturated solution of common salt, and this process is repeated three or four times successively. The last precipitate is dissolved in pure water, and the solution contains pure, typical, unchanged fibrinogen. On the addition of a little ferment the solution coagulates throughout. Fibrinogen is contained in hydrocele fluid, from which it can be precipitated by saturation with hydrocele.

Fibrin ferment.—This may be obtained by adding absolute alcohol to blood serum till the whole of the proteids are precipitated. The precipitate is collected and kept in absolute alcohol for at least a fortnight. The proteids are by this means rendered nearly insoluble in water, whilst the ferment, being unaffected by alcohol, can be extracted by means of water, mingled only with a very small quantity of albumin, from which it can be freed by the transmission of CO_2, or by the cautious addition of acetic acid. Blood which is made to flow directly from the vein into absolute alcohol contains no fibrin ferment; it is therefore generated after the withdrawal of blood from the body, and antecedently to the occurrence of coagulation.

The **serum of blood.**—The serum is the fluid that is gradually expressed from the clot by the contraction of the fibrin, and which accumulates upon

the clot. It may be regarded as the plasma minus fibrin, or one of the elements of fibrin. It is clear, transparent, and yellowish in a fasting animal, but opalescent after a full meal, owing to the quantity of chyle, containing minute fat drops, that has been poured into it. It has an alkaline reaction, chiefly owing to the presence of salts of sodium. Its specific gravity is about 1027. A thousand grammes of blood yield between 440 and 525 grammes of serum. It contains about 10 per cent. of solids, of which the most abundant are the proteids, and especially serum albumin (4 per cent.) and paraglobulin (3 per cent.), but it also contains many other organic compounds. The most important of these are sugar, urea, uric acid, and kreatin. The presence of sugar in normal blood may be demonstrated by the reduction of copper oxide in the usual way, and it seems probable that the sugar is either grape sugar or maltose. In nursing women the serum has been shown to contain lactose. Part of the sugar is derived from absorption by the veins of the alimentary canal, for Mehring found that on dieting animals with dextrin or starch, a substance could be obtained from portal though not from hepatic venous blood the reducing power of which was increased on boiling with dilute acids, and which was therefore either dextrin or maltose. The quantity of sugar in the serum is greatly augmented in diabetes. Urea is present in minute proportion, as are also uric acid and kreatin; cholesterin and lecithin, in small but variable quantity, are always to be discovered in blood serum.

Salts of the blood.—There is a remarkable difference in the distribution of the salts of the blood between the corpuscles and the plasma. Thus, 1000 parts of moist corpuscles yield (exclusive of iron) 8 parts of mineral matter, of which potassium forms 3·3 parts, phosphorus pentoxide 1·1 parts, sodium 1 part, and chlorine 1·7 parts, calcium, magnesium, and

sulphuric anhydride making up the rest; whilst 1,000 parts of plasma yield 8·5 parts of mineral matters, of which chlorine forms 3·6 parts, sodium 3·3, potassium only 0·3 part, with the rest made up as before.

The **gases of the blood.**—When blood is exposed to the vacuum of an air-pump, a considerable quantity of gas is given off, amounting to about half its volume, and to about $\frac{1}{100}$th of its weight. Thus, if 100 parts of blood drawn from the carotid artery of a dog be exhausted, the gases obtained from it show that at 0° C. and 1 m. pressure of mercury, it contains 17 parts of oxygen, 29 parts of carbonic anhydride, and 1·4 parts of nitrogen.

The quantity of *oxygen* contained in venous blood varies within wide limits; thus, the blood returning from quiescent muscles contains only 6 per cent., whilst in the blood of asphyxiated animals it may be almost entirely absent. A small part of the oxygen is simply absorbed, just as oxygen is absorbed by water; but by far the larger part is taken up, not in accordance with the law of Dalton, but as a result of the affinity of the hæmoglobin of the red corpuscles for it, and quite independently of pressure. The former portion is given off exactly in proportion as the pressure is diminished, but the second portion is retained when the temperature is low, until the pressure is diminished to about 20 mm. of mercury, when it is suddenly released by the hæmoglobin. Exposure of the blood to a pressure of 6 atmospheres causes but little increase in the quantity of oxygen absorbed. That portion of the oxygen which is associated with the hæmoglobin, is so loosely combined with it that it is given off on boiling, or by the transmission through the blood of other gases, or by the addition of various reducing agents, such as ammonium sulphide, hydrogen sulphide, and iron filings. The oxygen absorbed into the blood seems to be rendered active, or to be converted into

ozone, and the hæmoglobin is really an ozone carrier. This may be demonstrated by adding to oil of turpentine which has been exposed to the air, and which, therefore, contains ozone, some tincture of guaiacum. No change is visible, but if a little blood be added, the mixture immediately becomes blue, owing to the hæmoglobin abstracting ozone from the oil of turpentine, and parting with it to the tincture of guaiacum.

The *carbon dioxide* contained in the blood is in a state of chemical combination, since all fluids that simply absorb this gas have an acid reaction, whilst the blood is alkaline, and it appears to be combined with sodium partly as a carbonate and partly as a bicarbonate. The latter portion can be extracted by the air-pump alone, the former requires the addition of an acid. A small quantity is combined with the sodium phosphate, two equivalents of which take up one of CO_2, becoming changed into acid sodium phosphate and neutral sodium carbonate. The proportion of CO_2 in the blood may vary from 30 vol. per cent. in arterial blood, at 0° C. and 1 m. pressure, to 35 vol. per cent. in the venous blood of inactive muscle, and it may even rise as high as 52·6 vol. per cent. in asphyxia. Since 100 parts of blood may contain 30·5 vol. CO_2, yet 100 parts of serum of the same blood only contain 31·95 vol. CO_2, it is obvious that the corpuscles must also absorb and combine with some carbon dioxide, for if the carbon dioxide were combined exclusively with the salts of the serum, we should have to admit that in the above example the blood was composed of 95 per cent. serum, and only 5 per cent. of corpuscles, which is known to be incorrect.

Origin and destination of blood corpuscles.—There is good reason for believing that the corpuscles of the blood are constantly undergoing renewal, and that their individual life is brief. Hæmorrhages, even when very free, are soon repaired with-

out injury to the constitution, and Rindfleisch has calculated that the reparation which takes place in women during the intermenstrual period amounts to 175 millions of corpuscles per minute. From what part of the body do these new corpuscles proceed? Do they spring completely formed from the organ or organs in which they are produced, or do they undergo a process of development in the blood? On these points our information is not very precise; but there are facts which seem to show that in adult mammals the lymphatic glands, the spleen, the cancellous tissue of the bones, and perhaps other organs, as the retiform tissue of the intestines, and in the infant the thymus and the thyroid, furnish their quota towards the regeneration and renewal of the blood. It is possible that the different origin may explain the slight differences observed in the form and characters of the ordinary corpuscles, and that the corpuscles known under the various names of leucocytes, nuclei of origin, globulins, elementary corpuscles, and hæmatoblasts, may proceed from different organs. In regard to the duration of life of the corpuscles still less is known. Experiments, in which the easily recognisable blood of one group of animals has been injected into the veins of another, have shown that the corpuscles soon disappear, those of the dog when injected into a pigeon becoming greatly reduced in number in the course of a fortnight or three weeks, whilst those of the pigeon injected into the guineapig become unrecognisable in the course of a few hours. And it is probable that whilst some simply break down in the blood itself and dissolve in the serum, others pass to the spleen, and are there attacked by giant-cells by which they are destroyed.

CHAPTER III.

MOVEMENT OF THE BLOOD.

THE movement of the blood is requisite that new material and oxygen may be brought to all parts of the system, and that waste material may be carried away. It is effected by the heart, which is a muscular organ divided into four cavities, between which valves are so arranged that the blood can pass in one direction only. There are two auricles and two ventricles. The right auricle and ventricle receive venous blood, and transmit it to the lungs, where it parts with carbonic acid gas and water, and takes up O, and then returns to the left auricle and ventricle. This is termed the lesser or *pulmonic* circulation. The left auricle and ventricle receive the arterialised or oxygenated blood, and transmit it to the system at large, from whence it is returned to the right auricle and ventricle. This is termed the greater or *systemic* circulation. The heart, therefore, although to outward appearance a single organ, is in reality double, the two halves being united for economy of space, and beating simultaneously.

Action of the heart.—The heart beats about 70 times in a minute, and the phenomena that may be observed are the following: In the first place contraction and relaxation succeed each other in regular order. The period of contraction is termed the *systole* of the heart, the period of relaxation *diastole.* The two auricles contract simultaneously, then the two ventricles contract simultaneously, and then there is a pause. The systole and diastole together constitute one entire revolution of the heart's action. If the heart be

carefully examined *in situ*, in the chest of an animal from which the chest walls have been in part removed, it will be seen that the systole commences with a contraction of the great veins at the base of the heart, which rapidly extends over the auricle and ventricle. These become hard and prominent, the apex of the heart is tilted forward, and the whole heart moves downwards, becomes more uniformly conical, and turns a little to the right, so that more of the left ventricle is visible than before. The upper part, or base of the heart, descends to a small extent, but the apex remains nearly at the same level, because its descent, occasioned by the recoil of the great arteries, is to a great extent compensated by the shortening of the whole heart. At the same time the ventricular cone, which in diastole has an oblique position, now assumes a nearly vertical one. The cessation of the contraction is sudden, and the heart becomes flaccid. In the case of the auricles, the appendices are the first parts to contract. The impulse of the heart against the chest walls is coincident with the contraction of the ventricles. The duration of the several phases of the heart's action is, for the contraction of the auricles, a little more than one-tenth of a cycle; for the contraction of the ventricles, about four-tenths; and for the pause, which varies much more than either of the others, a little less than five-tenths.

The accompanying diagram shows the cardiographic tracings obtained by means of small elastic bags introduced into the cavities of the heart, and of a tambour applied to the chest wall. The upper line gives the variations of pressure in the right auricle, the middle line those of the right ventricle, and the lower one the impulse of the heart against the chest. The rise of the line shows an increase of pressure, and is indicative of contraction; its fall shows the period of relaxation and diminution of pressure.

From a study of these tracings, it may be seen that the auricle contracts before the ventricle, and

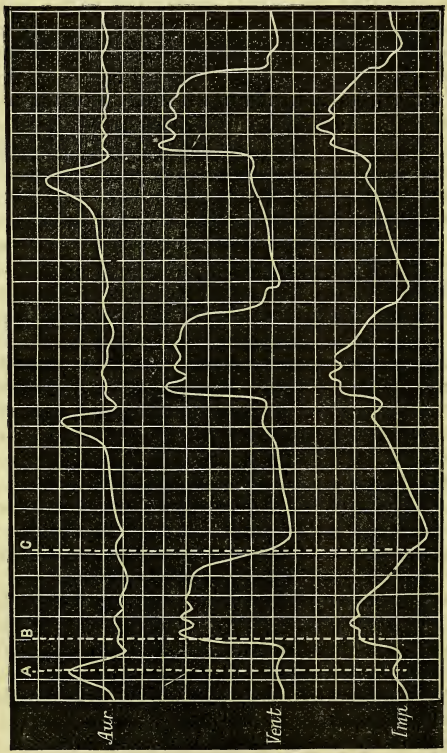


Fig. 2.—Tracings showing the Variations of Pressure in the Auricle, *Aur.*; in the Ventricle, *Vent.*; and of the Impulse of the Heart, *Imp.*

The dotted line A shows the instant of the auricular systole. B corresponds with the commencement and C with the termination of the ventricular systole.

that its contraction is not synchronous with the impulse of the heart, but precedes it. The contraction of the ventricle, on the other hand, coincides precisely

in point of time with the impulse of the heart. It is seen, also, that the systole of the auricle is sharp and short, the line rising suddenly, and as suddenly falling; the line remains low with some slight undulations, for some time, then slowly rising as the veins continue to deliver their blood into the auricle. It is seen, further, that the auricular contraction makes itself perceptible by a slight rise in the ventricular tracing; that the ventricular systole immediately follows, and is long sustained. By proper arrangements it may be demonstrated that the contraction of the two ventricles is precisely synchronous.

Course of the blood through the heart, and action of the valves.—The blood, during the period of diastole of the heart, swiftly fills the right and left auricles, and a certain quantity passing through the tricuspid and mitral valves, enters the right and left ventricles. The auricles then contract, and, owing to the peristaltic character of the contraction, which proceeds from the great veins towards the auricles, and then extends over the auricles themselves, drive the blood they contain into the ventricles, which become fully distended, and the edges of the tricuspid and mitral valves are brought into apposition. The ventricles now contract energetically, and their first effect is to render tense the auriculo-ventricular valves, which prevent any regurgitation of blood into the auricles; but the pressure still increasing, the blood forces open the previously closed semilunar valves, and is driven into the pulmonary artery and aorta. As the resistance to the opening of these flood-gates is great, the contraction is long and vigorous. The diastole follows, the heart returns to its former oblique position, and the recoil of the over-distended arteries effects the closure of the semilunar valves, and the whole cycle recommences. The reversion of the auriculo-ventricular valves into the auricles is effectually

guarded against by the contraction of the musculi papillares, which contract simultaneously with the walls of the ventricles, and thus tighten the cordæ tendineæ attached to the back and edges of these valves.

The *semilunar valves* seem at first sight to be almost too delicately formed to resist the whole backward pressure of the blood caused by the elastic recoil of the aortic or pulmonary vessels, but careful examination shows that the bottom of each pocket is formed by the muscular wall of the heart itself, and that the valves do not close the area of the artery by the mere contact of their edges, but that the whole surface of the lunulæ are brought into apposition with each other, and that consequently the stronger the backward pressure the more firmly are the valves pressed together, and the more perfect is the occlusion of the arterial opening.

In experiments made with the heart of the frog, it has been found that with over-distension of the sinus and auricle, even when the pressure is comparatively low, these parts of the heart become powerless to act, but as the pressure within is reduced they contract feebly, and when the quantity of blood flowing into them is only just sufficient to bring about full distension during diastole, they contract powerfully and empty themselves completely at each beat. As the supply of blood is further lessened, the contraction apparently again becomes feebler, and in the sinus hardly visible (Sewall and Donaldson).

Sounds of the heart.—When the ear is applied to the chest over the region of the heart, two sounds are heard; one dull and prolonged, which is the first sound; the second short and abrupt, which is the second sound. The causes of the first sound are essentially the vibration of the column of blood in the ventricles, and of the auriculo-ventricular valves when made tense by the contraction of the ventricles,

with the occurrence of which it coincides; and secondly, the sound produced by the muscular contraction of the walls of the ventricles. The composite nature of the causes producing the first sound has been demonstrated by Wintrich, with the aid of appropriate resonators; and although some objection has been raised as to the acceptance of the muscular sound as a cause of the first sound, on the ground that the contraction of the heart muscle has been shown to be a single shock, which is not sufficient to produce a series of vibrations recognisable as a sound, yet the very prolonged character of the contraction must be admitted to modify the conditions. The cause of the second sound is the vibration caused by the sudden tension of the semilunar valves, at the orifices of the aorta and pulmonary artery, the former of which closes from $\frac{1}{25}$th to $\frac{1}{20}$th of a second earlier than the latter. If these are hooked back by a bent needle introduced through the wall of the vessels, the sound ceases to be audible. That the sudden arrest of a moving column of fluid is capable of producing very audible vibrations is shown by turning a stop-cock in a tube through which water is passing, and thus abruptly stopping its progress. A loud sound and thrill may then be heard and felt over a large area. The first sound is most distinctly heard at the junction of the fifth rib with the sternum, and a little above and to the inner side of that point; the ventricular wall is here near the chest wall, and the moving column of blood in the ventricle conducts the sound towards it. The aortic element of the second sound is best differentiated at the attachment of the first rib to the sternum on the right side. The pulmonary element is heard most distinctly over the second intercostal space of the left side, just external to the border of the sternum.

The **impulse of the heart.**—This is the sensation which can be perceived with the eye and felt

by the hand when it is placed against the wall of the chest on the left side, and which is particularly evident when the fingers are pressed into the fifth intercostal space, in a circumscribed region about midway between the left edge of the sternum and a vertical line drawn through the left nipple. It is caused by the sudden pressure, due to the thickening, hardening, and tilting forward of the lower and anterior part, but not of the extreme apex of the heart in contraction against the wall of the chest. The pressure of the heart against the chest is aided by the recoil of the spirally-disposed first portions of the aorta and pulmonary arteries, which have been lengthened and straightened by their sudden distension with blood (Alderson, Barr). The impulse is most perceptible when the body is in the prone position, and in complete expiration. On the contrary, it becomes faint or imperceptible when the body is lying on the back and a full respiration is made, because the heart is then separated from the chest wall by the inflated lung.

Duration of the phases of the heart's action.—The contraction of the auricles lasts in a heart beating once in the second about $\frac{1}{10}$th of a second; the contraction of the ventricles endures for about $\frac{4}{10}$ths of a second. The duration of the pause, which term is a clinical one, and includes both the diastole of the heart and the auricular systole, was found by Landois, in a heart beating 55 times in a second, to last 0·577 sec., the diastole being 0·4 sec., and the auricular contraction 0·177 sec.; the systole of the ventricles lasted 0·34 sec.

The three accompanying diagrams (Figs. 3, 3*a*, 3*b*) represent tracings of the impulse of the heart, or cardiograms, as obtained (Fig. 3) by means of a Marey's sphygmograph, and (Figs. 3*a*, 3*b*) with Brondgeest's apparatus, in which the tracing is received on a plate connected with a vibrating tuning-fork. In the latter

case, the tracing presents minute undulations, each representing one vibration of the fork, and giving an instructive measure of time, which in this instance amounted to 0·01613 sec. Careful observation showed that the segment *b*—*c* was registered at the moment when the first sound was heard. It therefore corresponds to the systole of the ventricle, and to the

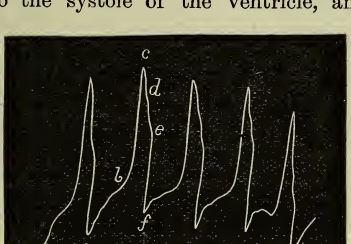


Fig. 3.—Cardiogram or Tracing of the Cardiac Impulse.

The rapid ascent of the line from *b*—*c* is produced by the contraction of the ventricles, and is coincident with the first sound of the heart. The line then suddenly descends, but shows at *d* and *e* slight elevations, which are synchronous with the second sound; *d* corresponding to the closure of the aortic, *e* with the closure of the pulmonary valves. From *e*—*f* corresponds with the period of diastole.

moment when the shock, or *ictus cordis*, was felt by the fingers over the cardiac region. During the registration of the tract *d*—*e* (Fig. 3), the second sound occurred; this portion of the curve therefore corresponds to the closure of the aortic and pulmonary semilunar valves. The small elevation *d*, when a double second sound is heard, is coincident with the closure of the aortic semilunar valves, and the indentation *e* with that of the pulmonary semilunar valves, the former closing first on account of the greater pressure exerted by the systemic blood; *e*—*f* represents the relaxation of the ventricles, and with the remaining segment *a*—*b* corresponds therefore to the pause and to

the contraction of the auricles, and is at first nearly horizontal and then presents a gradual rise. These determinations have been verified by applying the

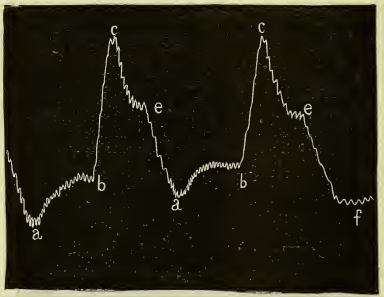


Fig. 3*a*.

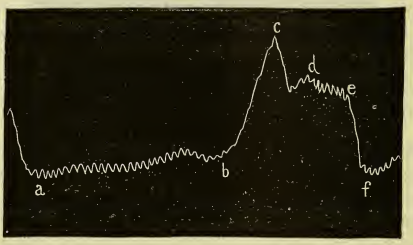


Fig. 3*b*.

Cardiograms taken with a Brondgeest's Apparatus.

instrument to the exposed heart of an animal in deep narcosis, in which artificial respiration is maintained. When the action of the heart is in any way hurried, the pause is found to become greatly shortened. In Fig. 3*a*, the four teeth lying over the first *a* and the two teeth over the second *a* are included in the pause;

then follows a slight wave-beat, seen in Fig. 3*b*, which Landois interprets as the expression of the contraction of the vena cava, vena pulmonalis, and auriculæ cordis; then there is a larger wave just before *b*, which is the contraction of the auricles; and then follows immediately the strong contraction of the ventricles, represented by the up-stroke *b*—*c*. The duration of the events taking place in the heart, as determined in this way, corresponds well with the times above-mentioned. In Fig. 3 the duration of the pause and the contraction of the auricles, when the beats of the heart were 74 per minute, amounted to 0·5 sec.; in Fig. 3*a* the corresponding tract *a*—*b* = 19—2 vibrations = 0·32 sec.; in Fig. 3*b* = 26 vibrations, corresponding to 0·42 sec.

Phenomena accompanying each phase of the heart's action:

1. *Events occurring synchronously with the first sound of the heart.*—At this moment (1) the ventricles contract. (2) The auriculo-ventricular valves are closed and rendered tense. (3) The semilunar valves are forced open, and the blood in the ventricles is propelled into the pulmonary artery and aorta. (4) The auricles are just beginning to dilate. (5) The impulse of the heart is felt.

2. *Events occurring synchronously with the second sound.*—(1) The semilunar valves are closed and rendered tense. (2) The auriculo-ventricular valves are open. (3) The auricles are filling, and some blood is entering the ventricles.

3. *Events occurring synchronously with the pause.*—(1) The blood during the first part of the pause is entering both auricles and ventricles. (2) During the latter part of the pause the auricles contract and fill the ventricles completely. (3) The auriculo-ventricular valves are open. (4) The semilunar valves are closed.

Frequency of cardiac pulsation.—Variations in the frequency of the beats of the heart are essentially due to shortening or prolongation of the pause, the period of contraction remaining tolerably constant. The frequency of the heart's beats bears a certain relation to the resistance offered to the exit of the blood from its chambers; with slightly increased resistance the beat is more rapid, but beyond a certain point becomes slower; with diminished resistance it is accelerated, hence it becomes very rapid when much blood is lost. At birth, the number of beats is about 140; at the expiration of the first year it is 120; at the end of the second year, 110; during middle life it varies from 70 to 80; and in old age it again becomes slightly accelerated. It is slower in man than in the woman. Position of the body distinctly affects it, the beats being about five per minute more numerous in the sitting than in the recumbent position, and ten per minute more numerous in the standing than in the sitting posture. This is probably the result of a greater number of muscles being called into play in the sitting and standing than in the recumbent position, for it is found that all active muscular exertion increases the frequency of the beats of the heart, probably by driving more blood to the heart, and thus stimulating it to more active work. The same explanation may be afforded of the increased frequency of the heart's beats that occur when active digestion is in progress, especially when alcoholic beverages are used in moderation, and the society and conversation are bright and cheerful. Increased temperature of the blood increases the rapidity of the heart's action, hence in part the rapidity of the pulse in febrile conditions of the system.

Force exerted by the heart.—The entire force exerted by the heart is very great. That of the ventricles has been estimated by Haughton at about

124 foot-tons daily; by other observers it has been given at upwards of 200 foot-tons. Speaking generally, the pressure of the blood which the heart drives determines the amount of work it performs, in the same way that weighting influences the work of other muscles; and, as in the case of other muscles, it is found that the work done by the heart increases with increase of weighting, that is to say, in this case of blood pressure, up to a certain point, after which it decreases. The work done in a given time is estimated by multiplying the volume of blood discharged by the pressure under which it is moved. Thus, if we consider that the left heart propels at each systole a mass of blood, the weight of which is estimated at about 180 grammes, or about $\frac{1}{400}$th of the weight of the body under a mean pressure of 250 mm. of mercury, which is equal to a column of blood 3·21 m. high, then the left ventricle is capable of lifting at each systole 180 grammes of blood to a height of 3·21 metres, that is to say, can do an amount of work equal to 578 grammeters. Admitting 72 pulsations per minute, we arrive at the total of 60,000 kilogrammeters as representing the work of the heart in 24 hours. If the work done by the right ventricle be estimated at one-fourth of this amount, the total work of the heart will be about 75,000 kilogrammeters. The work done by the heart is entirely converted into heat, in consequence of the friction which the blood undergoes in the circulating apparatus. The 75,000 kilogrammeters of work represent about 180 calories (425 kilogrammeters representing 1 calory), that is to say, the quantity of heat corresponding to the combustion of 20 grammes of carbon (1 gramme of carbon producing 8,080 calories in burning), or about one-fourth of the entire muscular exertion of a man doing a full day's work of eight hours, which amounts to three hundred and twenty thousand kilo-

grammeters (Fredericq).* The left heart having to drive the blood through the whole of the systemic capillaries, as well as through the double circulation of of the liver, is much more powerful than the right heart, which has only to propel the blood through the lungs. Hence the walls of the left heart are much thicker than those of the right, and, as might be expected, the left heart becomes thicker and stronger during pregnancy, when it has, in addition, to supply with blood the enlarged uterus and the placenta; on the other hand, in the fœtus, where the blood pursues a different course, the difference is less marked.

Does the heart dilate actively?—The ventricles empty themselves completely at every stroke, and it may often be seen on section after death, when the heart is fixed in systole by post-mortem rigidity, that the cavity of the ventricle, and of the left ventricle in particular, notwithstanding the irregularity of its shape, is completely obliterated. There is good reason for believing that the ventricles exert a considerable power of active dilatation, since it has been found that even after death the left ventricle of the calf, in expanding after compression with the hand, is capable of raising a column of water one foot in height. During life, strong evidence has been obtained that the aspirating power is far greater than this. Goltz introduced into the right or left ventricle of the dog, through the carotid artery or jugular vein, as the case might be, a thin-walled silver catheter, connected with a mercurial manometer by a tube, in the course of which was a valve opening either towards the heart or the manometer, according to whether the minimum or the maximum pressure was to be measured. With this apparatus he ascertained

* The force with which the blood is propelled from the left ventricle has been estimated to be equal in man to 2 kilos = 4 lb. 4 oz on the square inch, and in a horse to about 11 lbs.

that, with the unopened thorax, the negative pressure in the left ventricle of the dog may be as great as − 52 mm. of mercury; whilst for the right ventricle the negative pressure was, in one animal, − 16 mm. of mercury. After the thorax had been opened and the aspirating power due to the elasticity of the pulmonary tissue thus eliminated, he found that the negative pressure within the left ventricle rose in one instance to − 23·5 mm. of mercury. It is probable that this suction is exerted only for a short period during the commencement of the diastolic period.

Cause of the rhythmic action of the heart.—Is the rhythmic movement of the heart a property of its muscular tissue, or are the movements dependent upon a series of nervous impulses emanating in response to stimuli from nerve centres having opposite functions? The evidence seems to point to the presence and action of both these factors. In the first place, the heart of many of the lower vertebrates, when removed from the body, will, after a period of quiescence, prolonged sometimes for many minutes if kept under favourable conditions, commence to contract spontaneously, or at least without visible or recognisable stimulus, and continue to contract in a rhythmical manner for hours together. And again, parts of the ventricle or auricle, such as long strips or irregularly-detached portions, will contract in a similar manner. No doubt nerve ganglia are extensively distributed through the heart, and the nerves emanating from these ganglia form plexuses pervading the muscular tissue, so that a possible explanation might be given by reference to the ordinary mechanism of reflex action, in which a stimulus applied to an afferent nerve causes a nerve centre to liberate impulses that, travelling down an efferent nerve or nerves, excite a muscle to contract; but there are parts of the heart, as the apex of the ventricle, which are known in the

case of the frog to be entirely destitute of ganglia, and which exhibit, when removed or physiologically disconnected from the rest of the heart by a ligature, a manifest disposition to commence rhythmical contraction. Thus Bowditch has shown that if the ventricle of a frog be sharply compressed transversely with a narrow-bladed pair of forceps, the apex thus physiologically disconnected from the base remains quiescent, whilst the base continues to beat with its former rhythm. On clamping the aorta, however, the apex may once more be made to beat rhythmically, though slowly, the stimulus being the increased pressure experienced by it during the systole of the ventricle. In other instances, when the apex has been separated with the knife, though perfectly quiescent at first, yet if kept in a moist chamber it will often recommence to beat rhythmically, or can be taught to do so by applying an induction shock for a little while at regular intervals. Though all parts of the heart agree in the tendency to automatic contraction alternating with dilatation, some are more highly endowed with this property than others, the sinus venosus and auricle being much more active in this respect than the ventricle. Long ago Sir James Paget showed that a very small band of muscular substance allowed to remain as a bond of connection between the sinus venosus and the auricle, or between the auricle and the ventricle in the frog or tortoise, will enable the two parts, though otherwise severed, to preserve their ordinary and natural sequence of rhythm; hence, as Gaskell maintains, we may fairly eliminate the hypothesis that stimuli must necessarily pass from the sinus to the auricles and ventricles through the cardiac nerves and attached ganglia, and he holds that the function of the latter is to regulate the time of arrival of the stimuli at the ventricle, so that the ventricle may always contract in regular succession to the auricle.

For, in the first place, the due sequence of ventricular upon auricular beat is not in the slightest degree affected by section of all the nerve trunks between the sinus and ventricle, nor even by the complete removal of them with their accompanying ganglia. On the other hand, if the auricles be cut away from the ventricle, leaving only the coronary nerve as the link of communication between the sinus and the auriculo-ventricular groove, there is never the slightest disposition on the part of the ventricle and the auricle in connection with it to beat in response to the rhythm of the sinus and that part of the auricle in connection with it. Since, then, the sequence of ventricular upon auricular beat does not depend upon the transmission of stimuli along nerve fibres, from the starting-point of the rhythm to the auricle and ventricle respectively, what does it depend upon? The answer that may be given is, that the ventricle and auricle contract in orderly sequence because a spontaneously-arising wave of muscular contraction, commencing at the entrance of the great veins into the heart, passes along the auricle, and induces a ventricular contraction when it reaches the auriculo-ventricular groove. If, however, we go so far as to acknowledge that the muscular tissue of the heart possesses an automatic tendency to rhythmical action, which it can exert quite independently of the nerves, it is not less true that this action is ordinarily under the control and is always powerfully influenced by the nervous system.

The **nervous mechanism of the heart.**—The heart has nerve ganglia in its substance, and receives nerve fibres which are in communication with these ganglia, from the sympathetic and from the vagus nerves.

(*a*) *Intrinsic innervation of the heart.*—If, as already stated, the heart be removed from the body, and its nutrition be maintained by supplying it with

defibrinated blood, it will continue to contract rhythmically for some time. It has been argued, therefore, on this ground that it has a nervous system in its walls, which is capable of acting automatically, that is, of responding to excitations generated in the heart itself; and this view is no doubt supported by the results of microscopical examination, which shows that scattered ganglia are to be found in the substance of the base of the heart, and in the frog especially in the auriculo-ventricular furrow, and near the point of opening of the vena cava into the auricle. The apex of the heart, as already stated, contains no ganglia, and if this be severed from the heart, its movements cease whilst the rest of the heart continues to beat rhythmically. Ludwig hence concluded that the above-mentioned ganglia acted as centres. Stannius performed another experiment on the frog. He applied a ligature to the venous sinus leading to the right auricle, at the level of the ganglia that are found at this spot, which are known as the ganglia of Remak, with the result that the movements of the heart were at once arrested; but when he applied another ligature to the heart at the auriculo-ventricular furrow, where a second set of ganglia, known as the ganglion of Bidder, are found, the heart recommenced to beat. Stannius concluded that there were two kinds of ganglia at these points, the former, when stimulated, which he believed to be the effect of the ligature, presiding over the arrest of the heart's action, the latter, when stimulated, causing it to contract rhythmically. Others, however, admitting the facts given by Stannius, have given a different explanation; holding that the ligature does not act as a stimulus, but destroys the ganglia in question. On this view the ganglia of Remak are the motor ganglia of the heart, whilst the ganglia of Bidder are the arresting or inhibiting ganglia. Hence, when the ganglia of Remak are destroyed by the ligature, the

inhibiting ganglia act and the heart stops; whilst, when the action of these ganglia is abolished by the second ligature, the heart recommences to beat, in response to impulses emanating from scattered ganglia in the heart's substance.

(*b*) *Extrinsic innervation of the heart.*—The heart receives nerves from two sources: from the *vagus*, and from the *sympathetic*. It is not possible, however, to trace any particular nerve to the heart in the same way that the phrenic may be followed to the diaphragm, for the branches both from the sympathetic and from the vagus unite to form a plexus named the cardiac plexus, and often vary both in their number and size, appearing in some instances to supplement each other, so that the fibres probably pursue different routes, and make, now this, now that, nerve larger and more conspicuous. The chief known or named branches entering into the formation of the cardiac plexus are, first, those which proceed from the three sympathetic ganglia of the neck and the first dorsal ganglion, named respectively the *ramus cardiacus superior*, *medius*, *inferior*, and *imus*. A branch from the superior cervical ganglion sometimes attaches itself to the hypoglossal nerve, and after entering the descendens noni nerve is given off from that nerve to the plexus; but this is an inconstant nerve. Secondly, those which proceed from the trunk of the vagus, from the external branch of the superior laryngeal nerve, and from the pulmonary plexus of the vagus, though these last are not very constant. From the cardiac plexus *superficial nerves* are given off, some of which are connected with a small ganglion lying beneath the arch of the aorta, whilst others form the right and left coronary plexuses, which probably contain vasomotor nerves for the coronary arteries and sensory nerves for the pericardium. *Deep nerves* pass to the ganglia situated in the auriculo-ventricular

furrow, and along the septum of the auricles. The precise mode in which the intracardiac ganglia are normally stimulated is unknown, but it is certain that the endocardium is sensitive, since the slightest mechanical irritation of the inner surface of the heart excites contraction; the mere contact of the blood streaming into the cavities would consequently constitute such a stimulus and induce reflex contraction; increase of blood pressure, on the other hand, appears to stimulate the inhibitory fibres and slows the heart. It might be held that some stimulus, whatever it may be, is constantly acting on the cardiac ganglia, and that an inhibitory mechanism exists which dams up the current liberated, so that, like a Leyden jar placed at a definite distance from a discharging knob and supplied with a continuous current, it gives off a spark periodically when the tension rises to a certain height.

Inhibitory nerves of the heart.—The vagus has a special action on the heart, and this influence is of interest because it was the first known example in which a stimulus applied to a nerve supplying a muscle causes not contraction, as in most other instances, but relaxation, or rather seems to be able to prevent its contraction, thus exerting what is named an arresting or inhibiting influence on muscle. This action of the vagus on the heart was recognised in 1843 by the brothers Weber. They observed that when the vagus was stimulated the heart ceased to contract, and remained flaccid or in a state of diastole, and this has been found to be the type of many other cases. The relaxing influence is not exerted persistently, for after the application of the electrodes of a galvanic battery for a few seconds, the heart begins again to contract rhythmically. To produce absolute arrest of the action of the heart in mammals, as a rule, both vagi must be stimulated simultaneously, but in the frog and some other animals it is sufficient

to apply the electrodes to one vagus. In all cases during stimulation, not only is the frequency, but the strength of the beats of the heart is materially reduced. The inhibitory action is exerted both directly and reflectorially, as may be shown by direct pressure on the vagus in the neck, but more easily and distinctly by dividing the vagus on one side, and stimulating first the distal and then the proximal stump of the nerve; arrest of the heart's action occurs in both instances, in the former case owing to the impulse travelling peripherally to the heart, and in the latter instance to its passing upwards to the medulla oblongata, and then down the opposite nerve. One or two contractions of the heart, representing a latent period, intervene between the application of the stimulus to the vagus and the arrest of the cardiac beats. Division of the vagus on one side does not materially alter the heart's action, but division of both vagi causes acceleration. The vagal fibres appear to be easily exhausted, whilst the mechanism in the heart on which both vagi act is not easily exhausted, for it has been found that in dogs, rabbits, and frogs, if stimulation of one vagus be continued till it ceases to have any inhibitory effect, the usual effects are immediately produced on stimulating the opposite vagus, providing the stimulation of the whole inhibitory mechanism has not been continued too long.

Certain poisons, as curare, atropin, and nicotin suppress the action of the vagus on the heart, and anæsthetics generally diminish its inhibitory influence, which is fortunate, since it prevents the occurrence of arrest of the heart's action in operations accompanied by much pain, which is well known to depress the action of the heart. On the other hand, muscarin and digitalis excite the vagus and lead to arrest of the heart's movement, the former acting on the intra-

cardiac terminations of this nerve, whilst the latter stimulates the vagal centre in the cord.

Inhibitory centre.—The inhibitory fibres seem to arise from a *centre* situated in the lower part of the

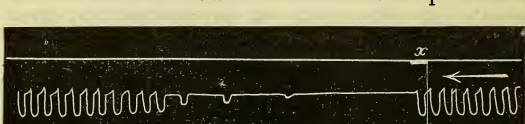


Fig. 3c.—Tracing showing the Effects of Short Tetanisation of the Vagus on the Beats of the Heart in the Frog. (After Foster.)

The beats were registered by means of a lever resting on the ventricle. The tetanisation at *x* lasted for about a second. The systoles recommenced in staircase fashion, and at some interval of time.

medulla oblongata, in common with those of the spinal accessory nerve, and to pass along the anastomosing

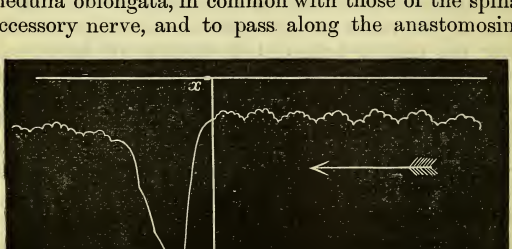


Fig. 3d.—Tracing showing the Effect of Short Tetanisation of the Vagus Nerve of the Rabbit on Blood Pressure. (After Foster.)

At *x* the tetanus was induced and lasted for about a second; a single systole, marked by the slight ascent of the tracing took place, the larger curves being due to respiration. The heart then stopped and the pressure fell; after a time it again rose and the beats recommenced.

branch between the two nerves into the vagus; since, if the spinal accessory be divided at its origin, the inhibitory power of the vagus in the course of a few

days can no longer be excited. It has been suggested by Schiff that the vagus is an ordinary motor nerve, which is, however, very easily exhausted, but the renewed rhythmical contraction during the continued application of the stimulus contradicts this view.

The *inhibitory centre* is excited (1) by a deficiency of blood, and therefore of oxygen, in the medulla oblongata, as occurs in sudden and great hæmorrhage; (2) by increase of blood pressure in the cavity of the skull, as may easily be shown by compressing the abdominal aorta of a rabbit, or by arresting the flow of blood in the great veins of the neck, and this influence of variation in blood pressure and quality of blood on the inhibitory centre is of importance, since it preserves the brain from excessive blood supply, and prevents also the heart from exhausting itself by too frequent contractions. The inhibitory centre may also be excited by increased venosity of the blood; hence the slight diminution of the frequency of the heart's action during the inspiratory phase of the respiration; (3) by mental emotions, as fear, joy, and surprise, all of which may lead to slowing or even to arrest of the heart's action.

The inhibitory centre may also be excited reflectorially: (1) By stimulation of certain visceral nerves; thus, if a frog be smartly slapped on the belly, the heart stops, though if the vagi be previously divided no such stoppage occurs; (2) by stimulation of almost any sensory nerve, that is, by pain; (3) by stimulation of the proximal stump of one vagus; (4) by sudden inflation of the lungs with atmospheric air, which lowers blood pressure.

Depressor nerve.—In the rabbit, horse, dog, and cat, and probably also in man, a small filament springs by two roots, one from the vagus, and the other from the superior laryngeal nerve, and applies itself to the sympathetic nerve. This nerve is sensory; if it be

cut, no effect is observed to follow stimulation of its peripheral extremity, but if the proximal extremity is stimulated the animal gives signs of pain, the heart's action is accelerated, and the pressure of the blood in the vessels undergoes remarkable diminution.

Accelerating nerves of the heart.—If the medulla oblongata, or the lower segment of the spinal cord, after its division in the neck, be stimulated, the heart's action is accelerated; an *accelerating centre* is therefore surmised to exist in this region. The acceleration takes place even after the division of the splanchnics, showing that it is not due to diminished tone of the vascular system generally, and there is evidence to show that the fibres which arise from the medulla oblongata and upper part of the spinal cord, and emerge from the cord by the lower cervical and upper dorsal nerves, to enter the first thoracic ganglion of the sympathetic, pass directly or indirectly into the cardiac plexus. A few fibres appear also to run in the trunk of the vagus, as may be shown by stimulating the distal stump of the divided vagus, after the inhibitory fibres have been paralysed by curare.

The action of the sympathetic nerve is in all instances augmentative, accelerating the rate of rhythm, increasing the strength of both auricular and ventricular contraction, and making the ventricle respond again in sequence with the auricles when that due sequence has been either impaired or abolished by clamping the tissue in the auriculo-ventricular groove (Gaskell).

The vigour and frequency of the heart's action are affected within wide normal limits by the quantity and quality of the blood traversing its cavities and supplied by the coronary arteries to its tissue. After fasting for a few hours only, the cardiac beats fall in number, the pulse is weaker, and the cutaneous veins may be seen to contain less fluid, whilst the circulation in them is slower. After a full meal, on

the contrary, when, owing to absorption, the quantity of blood is increased, and the pressure within the heart and vessels is increased, the opposite conditions are present. The influence of variations of pressure may be studied experimentally, and it would appear that, within certain limits, increase of intracardiac pressure diminishes, and may in fact entirely abolish, the cardio-inhibitory action of the vagus nerve, providing that such increased pressure acts both on the auricles and the ventricles. Internal pressure, therefore, has a stimulating action on the motor apparatus in the heart, which overcomes the retarding action of the vagus.

Staircase beats.—If, when the heart has been for some time quiescent, it is stimulated rhythmically, the beats are found to be at first feeble, and the rise of the tracing is low, but as the stimulation continues to be repeated the beats become progressively stronger, so that the curve presents a series of ascending steps, assuming at length their ordinary form. The step-like rise at the commencement of the stimulation has been termed "staircase beats," and the appearance in question is due, it is suggested by Kronecker, to the imperfect nutrition which he believes takes place during the protracted pause, and to which the heart, when normally contracting, is not exposed, since, with each systole, a fresh layer of blood is brought into contact with its inner surface.

The contraction of the heart is a single shock.—When a tracing is obtained of a cardiac contraction it is found to resemble, though it is of much longer duration, the contraction of ordinary muscle stimulated by a single electric shock; but it is remarkable that while ordinary muscle responds within certain limits by greater vigour of contraction to greater intensity of stimulus, the heart, as Bowditch has shown, if it respond at all, responds with all the vigour it is capable of exerting. As he expresses

it, a sufficient stimulus is always a maximum stimulus. The quantity of blood expelled at each contraction of the heart has been variously estimated at from three to five ounces.

The heart cannot be thrown into a state of tetanus.—If one of the ordinary striated muscles of the body, such as the biceps, or sterno-mastoid, be stimulated by a quick succession of electric shocks, it contracts rigidly and persistently, and is said to be tetanised; but if a similar succession of shocks be applied to the heart, although the beats are rendered more frequent by the shortening of the period of diastole, the muscular tissue does not pass into a state of tetanus, but continues to beat rhythmically, each contraction being instantly followed by a period of relaxation.

Refractory phase of the heart's action.—The excitability of the heart is not the same throughout the whole period of one revolution, for it has been shown by Marey that a stimulus which is effective if applied at one period, is inoperative at another. Thus, if a minimal stimulus be applied during systole, no increase of contraction is produced, it seems to be void of effect; but if the same stimulus be applied during the period of diastole, contraction immediately ensues. This period of diminished excitability he has termed the "refractory phase," and he has further shown that its duration is dependent on the strength of the stimulus, so that if a sufficiently strong stimulus be applied the refractory period or phase entirely disappears.

Marey has shown that this is not quite such an exceptional circumstance as at first sight appears to be the case, for even in such a muscle as the sterno-mastoid, the excitability of the tissue is diminished for a very short but appreciable period during contraction. During this period the muscle responds less energetically to a given stimulus, and it may be said to have a *refractory period.* In the heart the refractory period

is of longer duration, and stimuli applied just after the contraction has taken place fail to produce their proper effect till the tissue has, so to speak, gathered its forces together for the effort of a fresh contraction. If some part of the exposed heart of a frog be pressed somewhat firmly with a probe, this part will immediately contract with great vigour, but careful observation will then show that for several beats it remains quiescent. In other words, its refractory period is prolonged. It does not respond for a time to its normal stimulus.

CHAPTER IV.

BLOOD-VESSELS, AND THE DIRECTION OF THE MOVEMENT OF BLOOD IN THEM.

The blood driven out of the heart at each contraction of the ventricles, enters a system of tubes that is everywhere closed, except at the point where the great lymphatic ducts open into it; the tubes vary in structure, in accordance with the statements made in the companion volume to this, on "Histology," and are named respectively arteries, capillaries, and veins. The *arteries* dividing, but without intercommunication, carry the blood to every part of the body, and gradually break up into *capillaries*, or fine, hair-like vessels, that, freely anastomosing in the substance of each tissue and organ, supply it with blood, and then unite to form the *veins*, the function of which is to conduct the blood to the auricles; those commencing in the lungs ending in the left auricle, and those of the body at large in the right auricle, from which the blood passes into the corresponding ventricles to begin its circulation anew. The right auricle, right ventricle, pulmonary artery, pulmonary capillaries, and pulmonary veins form the pulmonary, or lesser circulation. The

left auricle, left ventricle, aorta, systemic arteries, capillaries, and veins terminating in the two venæ cavæ, form the greater or systemic circulation. In the exceptional case of the portal circulation, the great vein named the portal vein, formed by the coalescence of the veins arising in the intestines and other viscera of the abdomen, breaks up like an artery into smaller vessels, which again unite to form the hepatic veins, and conduct their blood into the inferior vena cava.

A second instance of a vein breaking up to form a capillary plexus, from which another vein arises, is afforded by the kidney. Here each terminal branch of the renal artery ends in an afferent vessel to a glomerulus. The efferent vein from the glomerulus, which corresponds to the portal vein of the liver, instead of combining with others to form larger veins, again subdivides into a plexus distributed over the convoluted portion of the renal tubules, from whence the blood passes to the renal veins.

The **arteries.**—The arteries are strong, highly elastic, and contractile, properties which they owe to their structure.

Their *strength or power* of resistance proceeds from the external sheath of connective tissue, which enables the vessels to resist without rupture the great distending force to which they are exposed at each systole of the heart, amounting, as Hales demonstrated, in the horse to the pressure of a column of blood eight or nine feet high; or to a column of mercury, as Ludwig has shown in the horse, 320 mm. in height.

Their *elasticity* permits them to yield, without danger of bursting, to the sudden increase of the strain upon their walls which occurs at each stroke of the heart, whilst it enables them to accommodate themselves easily to the various movements of the body. It has the further effect of converting the intermittent flow of blood in the large arteries, consequent on the

cardiac beats, into a uniform and constant current in the capillaries.

Their *contractility* confers upon them the power of adapting themselves to the variable quantities of blood they contain at different periods, and at the same time, as it is under the influence of the nervous system, it enables that system to control the amount of blood supplied to each tissue in accordance with its requirements.

Dr. Roy has pointed out a singular feature in the elasticity of animal tissues, and of the arterial walls in particular, in which they agree with caoutchouc, but differ from most other elastic substances, viz. that the elongation produced by weights is not proportionate to the weights employed, but, on the contrary, the increments in length diminish gradually in proportion to the weights. He finds, further, that when the arterial or venous wall, as well as some other tissues, are stretched, their temperature rises, whilst it falls again when they are relaxed. The elasticity of the arteries enables them to accommodate themselves to very different quantities of blood. Thus the capacity of the aorta of the rabbit was *quadrupled* when distended with an internal pressure of 200 mm. of mercury, as compared with its capacity in an undistended state. Different arteries, however, in the same animal always differ considerably, the capacity of the carotids under the same conditions as those just mentioned differing as 1 to 6. The pulmonary artery possesses the highest elastic distensibility in the body, for in more than one specimen of the pulmonary artery of the rabbit the capacity became, on raising the internal pressure up to 500 mm. of *water*, more than twelve times as great as that when undistended. The veins distinguish themselves from the arteries by the relatively small increase in capacity produced by raising the internal pressure from immediately above zero to 400 or 500 mm. of water, the increase being

usually about 1 to 2. The enormous changes in the capacity of the veins, well known to occur during life, are due less to differences of pressure than to the great differences in the quantity of blood they contain.

Agents aiding the movements of the blood.—The movement of the blood is promoted by several agents. First by the aspiration of blood into the thorax owing to the pressure in the chest being negative or below that of the atmosphere, even in expiration, and still less, therefore, in inspiration. To show that such negative pressure exists, it is only necessary to open the cavity of the pleura, when the lungs are seen to contract, proving that under ordinary circumstances they are permanently dilated beyond their natural state, and therefore must tend to draw the blood into the chest both by the venæ cavæ and by the aorta; but the effect is much more marked on the thin-walled veins than upon the thick and strong-walled aorta, and more blood would therefore enter by the veins even if there were no valves to the aorta. The circulation is further aided by the dilatation of the heart in diastole, and also by the compression of the veins possessing valves during muscular exertion. The influence of the valves is easily intelligible, for if a vein destitute of valves crosses a muscle, the muscle, becoming thicker on contraction, must compress it against adjoining parts, and tend to drive the blood in both directions; but if valves are present the backward flow is prevented, and the blood moves in the forward direction only. Lastly, the experiments of Roy have shown that various organs, such as the spleen and kidney, contract rhythmically owing to the unstriated muscle which is contained in their substance, which must tend to drive the blood onwards. The exquisitely smooth surface conferred upon the interior surface of the arteries, as well as upon the veins and capillaries, by the epithelial lining, facilitates the flow of blood by lessening friction.

Blood pressure.—The pressure of the blood in the vessels is the result of the force with which the blood is driven into them by the heart, and of the resistance that is offered to its onward movement. An old experiment, dating back to the time of Bernouilli, shows the gradual decrease of pressure in tubes with open mouths, and that there is an inclined plane or fall, the steepness of which indicates the

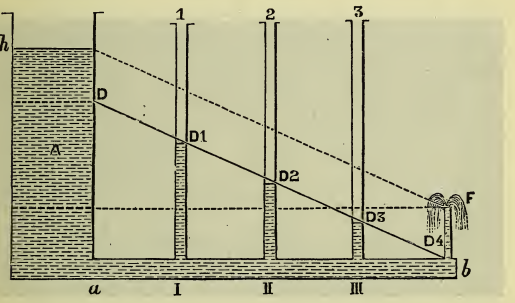


Fig. 4.—Diagram to explain the flow of fluids through rigid tubes, and the variations of pressure at different parts.

pressure of the fluid in each part of its course. If A in Fig. 4 be a cylindrical reservoir, filled to *h* with fluid, and *ab* a horizontal tube to which several vertical tubes, 1, 2, and 3, are attached, it will be seen that as the point of outflow F is reached the lateral pressure of the fluid against the walls of *a*, as measured by the height to which the fluid rises, D1 D2 D3, progressively falls. If F were closed the fluid would immediately rise in each of the vertical tubes to the level of the fluid in the cylinder A, and would remain stationary; but the moment F is opened the fluid begins to move, and its level in the several tubes falls in a diagonal line from the level *h* in the cylinder A to the level of the mouth of F; the fluid

would only again become stationary, if the discharge from F continued, when it had fallen in all the tubes to the same level as F. If, instead of the tube *b*F, the tube *ab* presented an open mouth at *b*, the fluid would of course continue to flow, and the pressure of the fluid in the vertical tubes would fall to zero. If we consider each of the vertical tubes separately, it is seen that the resistance in front counteracts part of

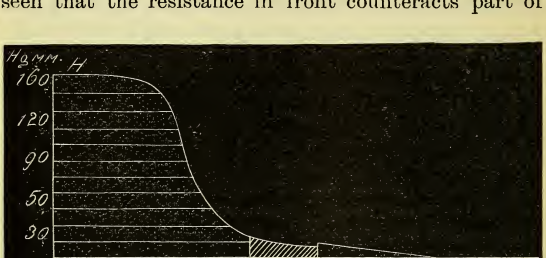


Fig. 4*a*.—Diagram to show the Variations of Blood Pressure in different parts of the Vascular system. (*After* Yeo.)
H, heart; A, arteries; C, capillaries; V, large veins.

the pressure exerted by the column of water in A, and that this resistance decreases towards the outlet. The resistance is attributable to the friction of the fluid against the walls of the tube, and this is necessarily greater at I than at II, and greater at II than at III. Hence the differences in the level of the fluid in the different tubes. If by means of a manometer the pressure of the blood be taken in different parts of the vascular system a very similar figure to the above is obtained (Fig. 4*a*).

It will here be seen that the pressure in the left ventricle of the heart is the highest in the body,

rising to 160 or more millimetres in the dog, and to as much as 300 millimetres in the horse. Moreover, this pressure is preserved in the larger arteries A, on account of the resistance offered to the passage of the blood by the smaller arterioles. Immediately beyond the smaller arterioles, however, the pressure rapidly falls, because the blood then enters the wide area of the capillaries. It becomes less in the veins, and in those near the heart actually descends below the basal line or zero, showing that there is some exhaustive or suction influence exerted upon it by the elasticity of the lungs, the diastole of the heart, or by the respiratory effort, or by all these combined.

If the arteries were a system of rigid tubes, and had no outlet on the side of the capillaries, it would be impossible for the heart to drive any blood into them, for fluids are incompressible, and no movement of the blood would occur; but the pressure of the blood against the walls would be increased during the heart's beat in exact proportion to the force of that muscle. If, however, instead of being rigid tubes, the arteries were elastic tubes, and had, as before, no outlet on the side of the capillaries, the heart would be capable of discharging its blood into them for a few beats, because the elasticity of the walls would permit them to yield and enlarge, but the pressure of blood would continue to rise at each stroke of the heart until the limit of their resistance was overcome and they gave way, or until the resistance offered to the entrance of more fluid was equivalent to the force which the heart could exert. But if, as is actually the case, the arteries are highly elastic tubes which terminate in a plexus of capillaries, it is clear that whilst at each stroke of the heart the pressure of the blood is raised throughout the arterial system, it must necessarily fall during the interval between two beats, because the blood is escaping by the capillaries. Pressure exists

against the walls of the vessels, because at any moment and in any part, except in the veins close to the heart, the quantity of blood contained in the vessels is greater than they can contain if their elasticity is not called into play, and the difference of pressure in different parts is practically the cause of the motion of the blood. The pressure in the aorta, termed the *blood pressure*, is greatly exalted at each stroke of the heart, but rapidly falls during the diastole as the blood escapes through its branches into the smaller arteries, and from thence into the capillaries. The *mean blood pressure* is the pressure which a manometer attached to the aorta would indicate when a line is drawn midway between the highest and the lowest pressure. The pressure necessarily falls in passing from the larger to the smaller vessels, because the resistance is lessened, a portion of the current being directed through lateral channels, and hence the *arterial pressure* or *tension*, which is the pressure exerted by the blood in any particular vessel, is determined by the force with which the heart drives blood into the arterial system, and the resistance which opposes the exit of blood from that system.

It is clear that the perfect action of the aortic semilunar valves is an important element in the maintenance of the blood pressure. If these are incompetent, that is to say, do not close perfectly, they will allow the blood which has just been forced into the aorta by the systole of the ventricle, to regurgitate. The result of this is, that the pressure suddenly raised in the aorta as suddenly falls, and a short sharp wave is transmitted through the system, which is sometimes named the "water-hammer" pulse.

The influence of the loss of blood on arterial pressure is remarkable; if only moderate in amount the effect is scarcely observable, for although the blood escapes readily from the arteries, and the result might

therefore be expected to resemble that of dilatation of the capillaries, and to be a fall of arterial pressure, yet this does not occur to a marked extent, because deficiency of oxygenated blood in the nerve centres stimulates them to action, and the smaller arteries everywhere contract, and thus the arterial pressure is maintained nearly at its normal amount. If, however, the loss of blood much exceeds 2 to 3 per cent. of the total weight of the body, the power of the heart fails, and the blood pressure suddenly falls.

The blood pressure can be, for a brief period, materially augmented by the transfusion of the defibrinated blood of another animal, which acts by filling the vessels and increasing the resistance offered to the introduction of more blood into them at each systole of the heart. The great size and distensibility of the abdominal veins enable them, however, to act as important regulators of the arterial pressure. Hence, when much fluid is added to the blood either by transfusion or absorption, it accumulates in these veins and the pressure falls, whilst when the general arterial system contains a deficient supply of blood, they contract and maintain the normal pressure by propelling the blood they contain into the general circulation. A remarkable experiment shows that this really occurs, for if the portal vein be ligatured, the blood continues to enter the abdominal veins, but is unable to escape, and so much may thus accumulate that the blood pressure may sink to zero, and the animal dies, having bled itself to death in its own visceral veins. If the ligature be relieved before this result occurs, the normal pressure is soon recovered.

The pressure of the blood steadily decreases in passing from the larger to the smaller arteries; thus, if in the carotid artery it is 150 mm., in the metatarsal artery it will not much exceed 100 mm. The reason that it falls to a certain extent is because the total

sectional area of the small vessels is greatly in excess of the primary trunk from which they are derived, and hence the blood is moving in a wider channel, and the only reason that it does not fall still lower is because the friction of the blood against the walls of the vessels is so much greater in the small vessels than in the larger ones.

Whatever increases the resistance to the flow of the blood through the vessels increases the pressure of the blood; thus, ligature of one or more large vessels, by diminishing the outflow in that direction, increases the pressure in the rest of the system. So, again, constriction of the smaller arteries, as by the action of cold, or by the irritation of vaso-motor nerves or centres, raises the pressure.

On the contrary, whatever facilitates the flow of blood from the arteries into the capillaries lowers the pressure of the blood in the arteries. Thus, warmth applied to the surface, by relaxing the small arteries, permits the large arteries to discharge their contents, and the pressure falls. The same result is seen after division of the vaso-constrictor nerves, as, for example, of the splanchnics.

The inhibitory action of the vagus normally regulates the blood pressure, since, whenever the arterial blood pressure rises above the normal amount, it constitutes a stimulus to the vagal centre, the immediate effect of which is reduction of the force and frequency of the cardiac beats and a return to normal pressure. The blood pressure of mammals seems to range between 100 and 200 mm. of mercury, though in exceptional instances it may rise much higher; in domestic birds it lies between 145 and 195 mm.; in tortoises between 30 and 50 mm.; in a frog it is about 30 mm.; in the eel about 70 mm.; and in the octopus about 80 mm.

Influence of the respiratory acts upon the circulation.—If a very deep inspiration be taken the heart beats more feebly, and may even be stopped,

an experiment that is sometimes called the "experiment of Müller." In like manner the heart may also be stopped if a very deep expiration be made. It is clear, then, that the respiratory acts exert a powerful influence upon the action of the heart and upon the circulation; and a little consideration will show that in regard to the *systemic circulation* inspiration must favour the diastole of the auricles and their distension with blood, whilst it must oppose a slight obstacle to the systole of the ventricles, and the passage of blood into the large arteries. The act of expiration, on the other hand, favours the systole of the auricles and ventricles, and presents a slight obstacle to the diastole of the auricles. As regards the *pulmonary circulation*, experiment has shown that the capacity of the vessels of the lungs augments, and a larger quantity of blood traverses these organs during inspiration than during expiration.

The action of the respiratory movements on the circulation in the arteries.—The large arteries contained in the chest respond to the variations of pressure that occur in the chest as the result of the respiratory movements. This is well shown in the following tracing, made by connecting an œsophageal sound with a

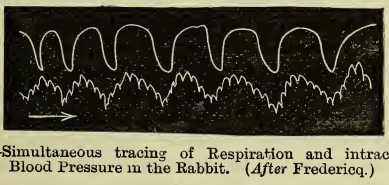


Fig. 46.—Simultaneous tracing of Respiration and intracarotidean Blood Pressure in the Rabbit. (*After* Fredericq.)

Marey's drum and lever; with each inspiration the pressure in the carotid is seen to fall, and with each expiration to rise. But as Fredericq has well explained, other influences aid in lowering the pressure during

inspiration. It has just been stated that the movement of venous blood to the heart is impeded during expiration, and that the right heart drives less blood into the lung than during inspiration. Moreover, the pulmonary circulation itself presents a greater obstacle to the passage of blood. But these circumstances, which no doubt diminish the outflow from the heart, and hence lower the arterial blood-pressure, require a certain time to propagate their effects to the left ventricle and aorta, in such mode that the retardation of the thoracic circulation due to expiration, and the diminution of arterial blood-pressure which results from it, coincide with the immediately succeeding inspiration and aid the direct mechanical action of the thoracic enlargement and dilatation. In the same way, the acceleration of the thoracic circulation which occurs in expiration really exerts its influence during the following inspiration, and aids in causing the pressure to rise. These effects may be clearly followed in those animals in which the respiratory acts are rapid; but if the respiration be slow, the arterial pressure, which falls at the commencement of inspiration, in part owing to the preceding expiration, may rise when the effects of the inspiration itself have had time to make themselves felt; and similarly the pressure may fall towards the close of expiration. A third factor here intervenes, which acts in opposition to the foregoing, though it is in general too feeble to make itself perceived, namely, the compression of the abdominal viscera and arteries by the descent of the diaphragm, which would naturally tend to raise arterial pressure during inspiration. In the case of the rabbit, the factors which cause the arterial pressure to vary during the act of inspiration are A, the mechanical action of the thoracic aspiration, which, as it causes the pressure to fall to a negative amount, may be expressed as $-A$; B, the changes in the thoracic and

pulmonary circulation, which, since they at first cause diminution and then increase of pressure, may be represented by ± B; C the compression of the arteries and viscera of the abdomen on the descent of the diaphragm, which tends to increase the pressure during inspiration, and is therefore + C. The sum of

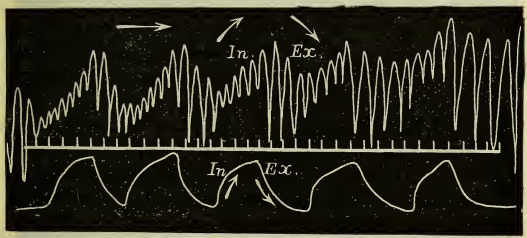


Fig. 4c.—Simultaneous Tracings of the Pulse in the Carotid, and of the Respiration in a large Dog, narcotised with Morphia, having the Chest opened and the Vagi intact. (*After* Fredericq.)

these three factors is negative during a short inspiration — A — B + C = — S; pressure low. But at the end of a long inspiration the pressure rises and the equation then becomes — A + B + C = + S. In the dog and pig, and in a slight degree also in man, two other factors (D and E) complicate the problem, namely, the rhythmically exerted influence of the respiration on the cardiac, and upon the vaso-motor centres. At each inspiration the inhibitory influence of the moderator or vagal centre of the heart is checked, and hence the beats of the heart are accelerated. During expiration the moderator centre is stimulated, and the beats of the heart become less frequent.

The respiratory acceleration of the cardiac rhythm (D) entirely masks in the dog the causes which tend

to lower arterial pressure, and on the contrary causes considerable increase of this pressure.

If by the administration of atropin, and the consequent paralysis of the intracardiac terminations of

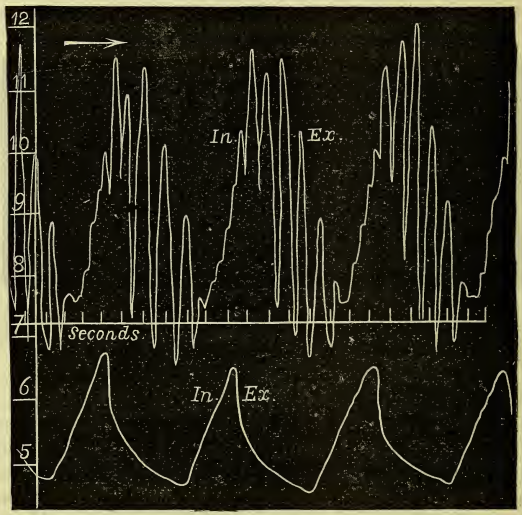


Fig. 4*d*.—Simultaneous tracings of the Arterial pressure taken by means of Ludwig's Kymograph, and of the Respiratory movements in the Dog, the latter taken with the pneumograph of Knoll. (*After* Fredericq.)

the vagus, the respiratory inequality of the cardiac rhythm be suppressed, or if by hæmorrhage or fever the action of the moderator centre is abolished, the discordance between the variations of the arterial blood-pressure and that of the pressure in the pleura immediately disappears.

This difference is well shown by comparing the

above diagram with the two following, in one of which the dog had been freely bled, and in the other poisoned with atropin.

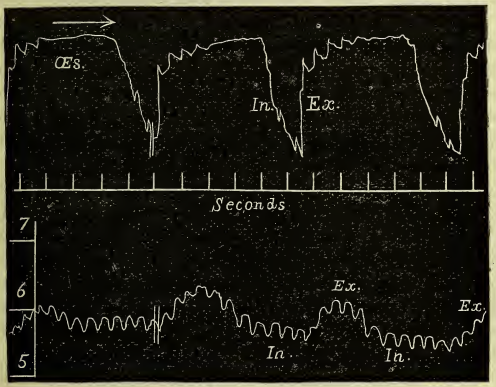


Fig. 4*e*.—The Respiratory variations of the Arterial pressure in a Dog after free bleeding, are shown on the lower line. The Variation of the intrathoracic pressure, taken by means of an Œsophageal Sound, is shown on the upper line. (*After* Fredericq.)

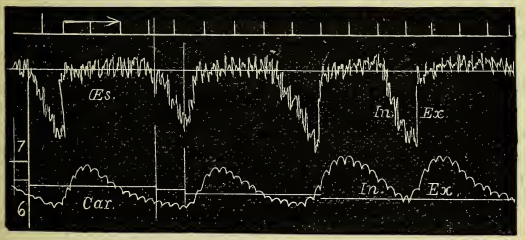


Fig. 4*f*. — The Respiratory Variation of the Blood Pressure in the Carotid of a Dog, poisoned with Atropin, is shown in the lower line. The Variation of the intrathoracic Pressure has been taken by means of an œsophageal sound, the ampulla of which rests against the Heart. (*After* Fredericq.)

E. the vaso-motor centre, presents, like the moderator centre of the heart, a rhythm isochronous with that of the respiratory centres. At each expiration all the small vessels contract, and consequently tend to augment the arterial pressure. At each inspiration they dilate, and therefore cause the blood pressure to fall. In order to render these oscillations of pressure due to vaso-motor influence evident, the thoracic and abdominal cavities of an animal must be laid open, and the phrenics and vagi divided. The respiratory movements are then only marked by slight separation and approximation of the ribs, but each inspiration is accompanied by a fall of pressure, and each expiration by a rise of pressure. These oscillations of the blood pressure are named the "curves of Traube-Hering." They are not seen in the rabbit. To sum up, the influences which in the dog act on the blood pressure in the course of a single inspiration are the following :

1. − A, the diminution of pressure due to thoracic aspiration.

2. − B and then + B, diminution of pressure in the first instance, followed by increase of pressure, owing to changes in the thoracic circulation.

3. + C, increase of pressure due to compression of the abdominal viscera.

4. + D, augmentation of pressure due to acceleration of the cardiac beats.

5. − E, diminution of pressure of vaso-motor origin. Traube-Hering curves.

In the dog the sum of the factors is positive, and results in an *increase* of the arterial blood-pressure.

− A ± B + C + D − E = + S.

The **pulse.**—When the finger is placed upon any artery and light pressure made, a beat or shock is felt, which is coincident with the systole of the heart. With each systole from three to five ounces of blood

are forced into a system of elastic already distended tubes, and a wave, which is quite different from the translation of the blood injected, is consequently propagated from one end of the body to the other. The whole arterial system becomes suddenly tightened and yields a little to make room for the additional quantity of blood forced into it. The pulse, as it is felt at the wrist, or on the temple, or on the dorsum of the foot, is the effort of the artery to recover its cylindrical form, when it has been compressed against the hard subjacent tissues, and temporarily flattened. The lateral expansion of the vessels is so small that it is inappreciable to the finger when they are surrounded on all sides by soft tissues. Hence, in operations, when it becomes necessary to tie a vessel, its pulsation cannot be felt unless it can be compressed against some hard tissue as bone. The wave excited by the systole of the heart, which must not be confounded with the onward movement of the blood itself, takes time to propagate itself to the more distant parts of the arterial system, as may be shown by the application of two sphygmographs to the limb, at parts as remote as possible from each other, and has been ascertained to vary, according to the condition of the arterial walls, from 6 to 12 meters per second, the velocity being somewhat greater in the vessels of the lower limb than in the upper, apparently on account of the more rigid nature of the walls of the vessels in the lower limb. For the same reason it is rather more rapid in old people than in youth. As the wave is propagated through the arterial system it becomes less and less marked. Strong, and of great amplitude in the aorta, it is gradually extinguished in the smaller vessels, and is ultimately lost in the capillaries.

The rapidity with which the pulse wave is propagated may be modified by two conditions. Every increase of resistance to the flow of blood by tightening

the vessels or raising the arterial tension accelerates the passage of the wave; but, on the other hand, this very increase of the arterial tension renders it more difficult for the heart to discharge its contents quickly. It propels less blood into the arteries at each pulsation, and the waves are of less volume, and are formed more slowly. On the other hand, when the arterial tension is low, that is when the arteries are less tightly filled, this cause of the slowing of the wave is compensated by the more easy and, consequently, more abundant and brisker penetration of the ventricular blood into the arterial system, and the waves travel correspondingly faster (Marey). And these two conditions usually compensate each other in health.*

Form of the pulse wave.—The form as exhibited in a sphygmographic tracing presents certain general features, whilst there are others which belong to the particular artery examined, to the character of the cardiac contractions, the quantity and quality of the blood, and to conditions of the system at large. The features common to all sphygmographic tracings of the pulse are a more or less sudden *rise of the line* indicating the commencement of the wave, a more or less pointed summit, indicating the period of greatest tension of the arterial wave, and an obliquely descending line indicating the gradual reduction of the arterial tension as the blood escapes from the arteries into the capillaries. The descending line usually shows a distinct secondary or dicrotic wave, and occasionally a third or tricrotic wave. The accompanying woodcut shows the form of the radial pulse of a healthy young person at rest, and is of a typical character. The systolic phase presents two inflections; the first, *b*, forming the summit of the pulsation, is at the end of the vertical

* According to Keyt, however, the rapidity of the wave is but little influenced by the state of the blood, nor by the frequency or force of the heart's action, and it is not materially modified by distance from the heart, nor by the branching of the main trunk.

line ; it does not constitute a sharp point as in those cases where the arterioles and their capillaries allow the blood to pass only with difficulty, and when the arterial system suddenly reaches its maximum of tension, but is rounded. This summit is followed by a wave *c*, which precedes the dicrotic wave *d*. The wave *c* has attracted much attention, and some authors hold their opinion in reserve, but Marey regards it as the end of the systolic phase, which in B is shown by a dotted

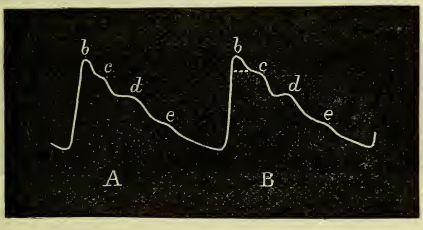


Fig. 5.—Type of Normal Pulse.
b, Primary wave; *d*, dicrotic wave; *c* and *e*, secondary waves.

line. The descending portion of the line corresponds to the diastolic phase of the pulse ; it expresses, by its more or less rapid fall, the greater or less rapidity with which the blood flows from or out of the arteries. The commencement of this is marked by the dicrotic rebound, which is never absent when the sigmoid valves are perfect, though its amplitude varies greatly. The number of subsequent waves increases with a rare pulse and high arterial tension, but they are suppressed with the entrance of a fresh wave from the heart. Fig. 6 exhibits three sphygmographic tracings of the pulse. When the heart discharges its blood into the arteries briskly the line of ascent is nearly vertical, for the recording cylinder of the sphygmograph has had but little time to move before

the artery has attained its greatest tension. When the blood enters more slowly the line of ascent is oblique, for the cylinder has had time to move before the period of greatest tension has arrived. The line may still be oblique if, by reason of the facility with which the blood escapes from the arteries into the capillaries, some time elapses before the arteries become quite distended. The ascending line may present an undulation, as in cases of insufficiency of the aortic valves, and in cases of the atheromatous arteries of advancing age, in which the elasticity of the wall is

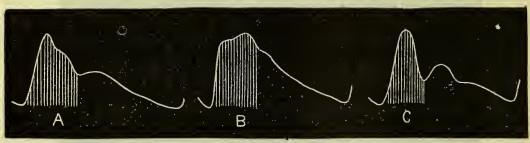


Fig. 6.—Three Sphygmographic Tracings of different form. In each the period of Ventricular systole is marked by vertical lines.

diminished so that it reaches its limit before the systole is completed, and the heart drives out the last portion of its contained blood with a protracted effort.

The *summit of the curve* indicates the period of greatest tension of the arterial wall, and if flattened or rounded shows that a condition of equilibrium has been established between the afflux and outflow of blood from the arteries.

The *descending line* indicates the diminution of arterial tension; the period of systole or diminution of calibre of the arteries, and the escape of the blood from these vessels into the capillaries. Its chief feature is the secondary rise, or dicrotic wave. This wave is caused by the sudden closure of the sigmoid valves. As the time which the wave occupies in traversing its own length is equal to the duration of the exciting cause, which is the contraction of the systole of the

ventricle, and which is known to occupy about $\frac{1}{3}$ of a second, the length of the wave, supposing it to move at the rate of 6 meters per second, would be $6 \div 3 = 2$ meters. But the distance from the heart to the most distant capillaries is never equal to 2 meters, the whole of one wave, therefore (from one crest, that is to say, to the next), is never in the arteries at any one moment. When the systole of the heart is completed, and the ventricle has propelled the whole of its blood into the aorta, the primary pulse-wave is propagated throughout the system; but instantly succeeding to this, the elasticity of the highly elastic aorta, over-distended with the blood just driven into it, begins to act, and tends to force the blood both forwards and backwards, but the backward movement is promptly stopped by the closure of the sigmoid valves, and a rebound of the blood takes place from them, analogous to the shock which is felt when a tap through which water is running is suddenly turned. This shock is shown by the dicrotic rise in the descending line of the sphygmographic curve. If the sigmoid valves are held back it vanishes. It is rendered more prominent by the sudden entrance into the aorta of the ventricular wave, by the small volume of this wave, and by feeble arterial tension. The conditions under which several secondary waves may be observed are, when the pulse is slow and the arterial tension is high.

The volume and strength of the pulse depend on the force of the cardiac beats, the quantity of the blood, the degree of arterial tension, and the greater or lesser elasticity of the arterial walls. *Cœteris paribus*, if the heart beats strongly, the pulse is large and full, as in a healthy man after moderate exercise. In certain inflammatory affections, on the other hand, as in peritonitis, the action of the heart is depressed, and the pulse becomes small and weak. In old people the arteries become rigid, their elasticity quickly reaches

its maximum, and the heart is feebler than in youth. Hence, the pulse is sharp and comparatively weak; yet, because the firm walls of the vessels are not easily compressed, it is hard. A cold bath, by driving much blood from the capillaries of the skin into the rest of the system, and thus increasing arterial tension, renders the pulse small and hard; whilst a warm bath, by facilitating the passage of blood from the arteries into the capillaries, lowers the arterial tension and makes the pulse full and soft. Mere alteration in the position of a limb will even cause a difference in the character of the pulse in it. Thus, if the arm be raised the pulse becomes more distinct, and the amplitude of the sphygmographic tracing is greater, because arterial tension is diminished, whilst if the arm be lowered, the pulse tracing becomes almost a continuous straight line, with but trifling elevations and depressions, because the tension is increased. Lastly, hæmorrhage, before the heart is exhausted, greatly increases the amplitude of the sphygmographic tracing by lowering arterial tension.

Duration of one complete circuit of the blood.—There is evidence to show that when a salt, such as ferrocyanide of potassium, is introduced into one jugular in the dog, it reappears in the opposite jugular in the course of about fifteen to twenty seconds. During this period it must have travelled to the right heart, have been transmitted through the lungs, returned to the left heart, circulated through the systemic arteries, capillaries, and veins of the head, neck, and upper extremities, and must be on its way again to the right heart.

The **velocity of the blood current.**—The velocity with which the blood moves in the vessels has been estimated in various ways. In the first place (1) there is the method of Blake, just described, in which the time occupied in the passage of a particular

salt, as potassium ferrocyanide, from one jugular to the other is determined ; in the horse it traverses the double circulation in thirty seconds ; in the rabbit, in seven seconds. Professor Robert Smith has, however, shown that the nature of the substance introduced into the vessels materially affects the apparent time in which the circulation is completed. Thus, when potassium ferrocyanide was introduced into one jugular vein of a dog, it appeared in one case in the opposite jugular in 15 seconds, or in 16 beats of the heart, and in another case after only $9\frac{1}{2}$ seconds with 14 beats of the heart. When, however, instead of a diffusible salt some defibrinated pigeon's blood was injected into one jugular, the corpuscles of which are readily recognised by their oval form and by their nucleus, the circulation was not found to be completed under 20 seconds with 55 pulse beats, and in another case under 17 seconds with 53 beats. But this only gives the duration of the circulation as a whole, and affords no indication of the time occupied by the blood in passing through any particular vessel, whether artery, capillary, or vein. For this purpose special instruments have been devised. In the arteries and veins the rapidity of the blood current may be approximately determined : (2) By the *hæmodromometer* of Volkmann, in which by a simple arrangement the current of blood coursing through a tube of glass inserted between the extremities of a divided artery can be suddenly diverted into a long bent tube, also made of glass, and the rapidity of its passage noted. (3) By Ludwig's *stromuhr*, in which the time occupied in filling a tube of known capacity is measured. This is the method that is generally employed, and is regarded as being the most trustworthy. Two pear-shaped glass vessels, united above by a common neck, and known when filled to a certain mark to contain a definite quantity of fluid, are inserted below into a brass disk, which

revolves air-tight upon the smooth surface of another piece of brass to which two tubes are attached. The disk and plate are perforated in such a way that a communication can be established between the tubes and the interior of the glass vessels. One of these tubes is placed in the proximal, the other in the peripheral portion of the divided artery, so that the blood can be made to traverse the two flasks. The glass vessel connected with the peripheral end of the vessel is filled with defibrinated blood, the other with oil. The blood is admitted, and the time it takes to drive out the defibrinated blood is noted; on reversing the plate the blood may be made to flow through them in the opposite direction, and the time again taken. (4) By Vierordt's *hæmatachometer*, in which a small cell, from the upper wall of which a light ball is suspended, is introduced between the cut ends of an artery; the deviation of the ball from the perpendicular shows the strength of the current. (5) By Chauveau's hæmodromometer, in which a short tube of glass occupies the interval between the cut extremities of the artery, and has in its interior a small circular disk to which is attached an indicator that passes through the wall of the tube and registers its movement on a scale; the wall is the fulcrum, the current of blood acting on the disk moves it in one direction and the indicator moves in the other. (6) By Chauveau's hæmodromograph. (*See* "Physiological Physics.") By any of these methods it is seen that the flow of blood is continuous, but undergoes great periodical accelerations. It is swifter in the large arteries than in the small, because the sectional area of the small arteries is much greater than that of the larger; the stream, taking them collectively, is wider, and the friction is greater. Any obstacle, such as constriction, presented to the passage of the blood in an artery retards the current of blood in that artery, whilst it

accelerates it in the other vessels. The following diagrams from Marey show this clearly. The first (Fig. 7) shows that whilst there is a great increase, indicated by the sudden ascent of the line, in the



Fig. 7.—Speed of the Blood Current, showing its sudden increase with each systole of the ventricle, and its arrest when the artery is compressed.

swiftness of the blood current at each systole of the heart, yet that it still continues to flow as indicated by the elevation above the zero line of the line connecting two waves, during the intervals of the pulsation, whilst it is stopped altogether when the artery is compressed, the line falling to zero. The next (Fig. 8) shows the speed of the blood current in one carotid when

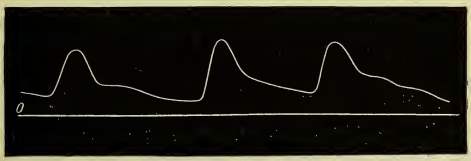


Fig. 8.—Tracing of the Speed of the blood current in the right carotid of a Horse when the left carotid is free.

the other is free, and the third (Fig. 9) shows the sudden and great augmentation, as indicated by the height the tracing as a whole has risen from the basal line, when the opposite carotid is compressed. The rapidity with which the blood moves in the carotid artery of the horse has been estimated at about

300 mm., or one foot, per second; in the maxillary of the horse, 165 mm., or between 6 and 7 inches, per second; and in the metatarsal artery of the same animal about 56 mm., or 2 inches, per second. These estimates are probably all too low. Speaking generally, everything which increases the force

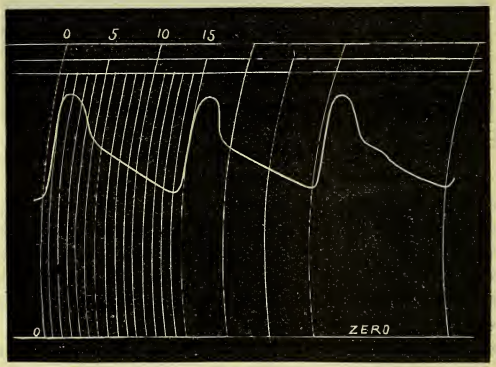


Fig. 9.—Tracing of the Speed of the Blood Current in the Right Carotid of a Horse when the Left Carotid is compressed.

propelling the blood towards the periphery increases the speed of the blood current and the arterial tension, and *vice versa*. On the other hand, everything which increases the resistance that the blood experiences in escaping from the arteries diminishes the speed of the blood current but increases the tension.

Movement of the blood in the capillaries.—The circulation in the capillaries may be seen in the web of the frog's foot, in the tongue of the frog, and in the mesentery of various small, warm-blooded animals placed with suitable precautions against desiccation

under the microscope. In the smallest capillaries the blood corpuscles may be seen moving in single file, separated from the wall of the vessel by only a very thin layer of fluid. Some pursue a straight course, others enter some of the numerous lateral and anastomosing channels that exist between the capillaries. At the point of bifurcation of the vessel the corpuscles sometimes hang poised, as it were, for a moment, and then press on to right or left. Certain capillaries become smaller as they are watched, others increase in size in accordance with variations in the size of the small arteries leading to them. The constriction and diminution of the lumen is produced by the cells composing the wall of the vessel becoming thicker, and thus encroaching upon the cavity. In the larger capillaries, where two or three files of corpuscles have room to move abreast, the comparatively heavy red corpuscles will be seen to occupy the middle of the stream, whilst the relatively light white corpuscles roll more slowly along in the lateral and slower current of the liquor sanguinis. It has been found, by experiment, that the difference in their specific gravity leads to this difference in their position; for Schklarewsky has demonstrated that when a fluid containing particles of different densities is propelled through capillary tubes, the heavier particles move with the greatest velocity and occupy the centre of the stream, whilst the lighter particles move in the peripheral portions of the stream and have a slower motion. The motion of the blood in the capillaries is uniform, and the flow continuous, no trace of the pulsation in the larger arteries, except under very peculiar circumstances, being perceptible. The pulsation has, in fact, been extinguished by the elasticity of the arteries and by the wider area formed by capillaries as compared with the arteries. The rapidity of the movement of blood in the capillaries is about 0·5

to 1 mm., or from $\frac{1}{50}$th to $\frac{1}{25}$th of an inch in a second. The pressure of the blood in the capillaries, determined by the indirect method of ascertaining what pressure will empty the capillaries beneath the finger nail, has been found to vary, according to the elevation of the arm, from one-fifth to one-half of the ordinary arterial pressure.

Automatic contraction of the smaller vessels and capillaries.—The capillaries appear to undergo periodic changes of diameter, admitting now a larger, now a smaller volume of blood, quite independently both of the beats of the heart and the acts of respiration. These changes are probably due to alternate contractions and relaxations of the smaller arteries dependent on the unstriated muscular tissue contained in their walls. In cases of disease of the mitral valve, when blood regurgitates into the left ventricle, and where consequently the arterial tension is low, the rhythmic variation in diameter of the capillaries can easily be demonstrated; for if, in such cases, the finger nail be drawn once or twice up and down the forehead, a red streak is left which lasts for some minutes, and it is then seen that the streak varies in width and brightness, not only with the beats of the heart, and with the respiratory acts, but with another rhythm which occurs about three times per minute. The proportion of the three rhythms would, therefore, be: automatic rhythm, 3; respiratory rhythm, 18; cardiac rhythm, 72 per minute (Brunton).

Movement of the blood in the veins.—The current of the blood in the veins is formed by the union of the currents from thousands of capillaries, which, now running in narrower channels, move more rapidly because the friction is reduced. The current is uniform, and free from the pulsation observed in arteries. The only exceptions to this are the pulsations in the larger veins of the neck, due to regurgita-

tion of blood into them during the systole of the right auricle, and the pulsations observed when the capillaries are greatly dilated and allow of an extraordinarily free current of blood through them. The heart is still the main driving force, but it is assisted

(1) By the aspiration to the chest occasioned by the negative pressure or tendency to a vacuum which is there present, and which is clearly and sometimes fatally shown by the rush of air towards the heart when one of the veins is opened.

(2) By the suction power exerted by the heart during diastole.

(3) By movements of the voluntary muscles, which, pressing on veins provided with valves, favour the onward movement of the blood, its regress being prevented by the valves.

(4) By position of the limbs, which act in a similar manner. Thus Braune saw the veins beneath Poupart's ligament collapse and the pressure become negative when the thigh was rolled outwards; but fill, and the pressure become positive when the limb was placed in its former position.

(5) By gravity, which acts, not primarily on the movement of the blood, but upon its distribution, and therefore secondarily upon its movement.

The pressure of the blood against the walls of the veins is everywhere low, and gradually diminishes from the smaller to the larger veins. In the brachial vein it will support a column of mercury 9 mm. high, but in the larger veins at the root of the neck the pressure is negative. It varies from -2 to -3 mm. synchronously with the heart's action, being of course increased during the systole of the heart when its flow into the auricle is temporarily arrested, and from -5 to -8 mm. with the respiratory acts, being increased during expiration. The rate of the movement of the blood in the large veins is probably slower than in the

arteries in proportion to their relatively larger sectional area. It has been estimated at 100 mm., or 4 inches per second, in the jugular vein of the horse.

Automatic contraction of the veins.—The veins, even when of large size, as the pulmonary vein and the vena cava, pulsate rhythmically, independently of the heart's action. Luchsinger found that when artificial circulation was maintained in the wing of the bat, distinct pulsation could be observed in the veins twenty hours after death ; and, therefore, long after the functional action of the nervous system was lost. If the pressure of blood was allowed to sink to zero, the pulsation stopped ; but recommenced when the pressure was raised to 40 centimetres of water.

Distribution of the blood.—In the living rabbit, when at rest, the experiments of Ranke seem to show that the whole mass of blood may be divided into four parts, of which one part is contained in the muscles, one in the liver, one in the heart and great vessels, and one in the remaining organs. Functional activity, however, causes an immediate increase in the quantity of blood circulating through a part, the augmentation sometimes amounting to as much as 47 per cent., which may be estimated by the plethysmograph. Such blood is, of course, taken away from other parts. Hence during physical exercise the muscles are largely supplied with blood, whilst the brain and digestive organs receive less, which teaches that neither severe bodily nor mental exertion should be made immediately after a meal.

Diapedesis.—Under certain circumstances, both white and red corpuscles may escape from the vessels, and pass or wander into the adjoining lymphatics. The escape of white corpuscles appears to occur normally, whilst the escape of the red only occurs when the pressure of the blood against the walls of the capillaries is much increased, or when there is retardation

of the blood current, as in inflammation. In the case of the white corpuscles, the attraction between the corpuscle and the capillary wall seems to be increased, the corpuscle begins to bore its way through the wall, assumes an hour-glass form, part being within and part without the lumen of the vessel, and it finally escapes altogether into the adjoining tissues.

The provisions for preventing death by bleeding.—As the blood-vessels form a continuous system of closed tubes, it would seem likely that if any of them were opened blood would continue to escape till death ensued. Experience shows us, however, that cuts, lacerations, punctured wounds, and contusions of considerable severity are not necessarily mortal, and several circumstances aid in controlling and arresting the hæmorrhage. These are contraction and retraction of the coats of the vessels, coagulation of the blood, and failing action of the heart inducing faintness. The contraction of the walls of the vessels is effected chiefly by the circular muscular fibres they contain, which, directly stimulated by the injury, diminish their calibre, and may *per se* altogether arrest the flow. The retraction is effected partly by the contraction of the longitudinal muscular fibres, but chiefly by the elastic tissue of the arterial tunics. The tunica intima in particular is found to curl back, and, by occluding the opening, to greatly aid in preventing the escape of blood. The withdrawal of the mouth of the vessel from the wound into the connective tissue by which the vessel is surrounded acts favourably in promoting the coagulation of the blood. Lastly, pain, fear, and, indeed, the mere sight of blood in most people occasions faintness, the heart beating with great feebleness, whilst the whole arterial system contracts, as is indicated by the pallor of the surface, and time is thus given for the formation of a clot, and the more perfect occlusion of the parted mouths of the cut vessels.

In the case of the veins, the valves materially assist in preventing any large escape of blood. In the case of subcutaneous hæmorrhage, such as occurs from contusions and the bursting of blood-vessels into confined spaces, such as the cranial cavity, the tunica vaginalis, or a joint, bleeding ceases in part owing to the pressure of the effused blood itself on the walls of the ruptured vessels, and upon the adjoining tissue. The scientific methods for arrest of hæmorrhage are placing the part in an elevated position, and thus taking advantage of the force of gravity pressure at the seat of injury; pressure or ligature applied to the vessels leading to the seat of injury; various agents acting as styptics, either locally or generally, such, for example, as cold, heat, perchloride of iron, and ergot, and the administration of remedies that, like tartar emetic, lower the action of the heart.

Transfusion of blood.—When much blood is lost from the body, the heart beats with great frequency owing to the diminution of the blood pressure, and very feebly owing to the insufficient supply of blood to the nerve centres and to its own muscular substance; and when the quantity is reduced below a certain point, convulsions take place. The occurrence of convulsions is the precursor of death, and life can then only be preserved by transfusion. The blood transfused should be withdrawn from an animal of the same species, and may be practised in cases of emergency with the simplest means, a lancet and a syringe, though where time is of no consequence many precautions should be taken. The blood should be withdrawn from a healthy man to the extent of half a pint or more; it may be whipped to defibrinate it; and it should be kept warm; one of the veins of the arm being opened, it may be injected slowly by means of the syringe, avoiding as far as possible the introduction of any bubbles of air, which are exceedingly

dangerous. Kronecker has lately revived dogs which had been bled to death by injecting a kind of artificial serum made of water, to which a little salt had been added; and frogs, it is well known, may be kept alive for a long time after their blood has been wholly replaced by a normal saline solution.

Peculiarities of the circulation in different regions.

(1) *The lungs.* — The pulmonary circulation is peculiar in having its capillaries, unlike those of the system generally, always under negative pressure, which varies according to the different phases of the respiratory acts. In *inspiration* the mean blood pressure diminishes in all the parts contained in the thorax, heart, and large vessels. This diminution of pressure favours the current of blood in the venæ cavæ, right auricle, and right ventricle, whilst it is opposed to the discharge of the arterial blood from the left ventricle through the aorta. The extensibility of the venæ cavæ is, however, much greater than that of the aorta, which is comparatively a rigid tube; hence the venous current is favoured, whilst the arterial current is but little interfered with. *Expiration* exerts an opposite influence. Pressure augments in the veins and in the arteries. The capacity of these vessels, and especially of the large intrathoracic vessels, diminishes; the arterial circulation is favoured whilst the venous circulation is rendered slower, and the heart receives less blood.

(2) *The brain.*—The four large arteries supplying the brain with blood, namely, the two internal carotids and the two vertebrals, anastomose with extraordinary freedom, so that a ligature applied to one of them does not materially interfere with the nutrition of that portion of the brain which ordinarily receives its supply of blood from it. The capillaries are very minute, and in the pia mater have a special sheath.

The skull, being a closed cavity, retains a considerable quantity of blood, even when, from hæmorrhage, other parts of the body are ex-sanguine.

(3) *The liver.*—The peculiarity of the circulation in the liver is that its main supply of food is obtained, not from an artery, but from a vein, the vena portæ, which receives the blood returning from the alimentary canal and its appendages, and forms a minute plexus of capillaries in the lobules, where it is joined by the capillaries of the hepatic artery. The hepatic veins arise from the plexus into which the portal vein has divided, and conduct the blood which has circulated through the liver, to the vena cava inferior. The blood of the mesenteric, splenic, gastric, and other visceral arteries, passes therefore through two series of capillaries before reaching the hepatic veins, one in the walls of the intestines, and in the substance of the spleen, and one in the liver. The circulation in the liver is necessarily slow. The blood traversing its vessels certainly contains much new material, directly absorbed from the alimentary canal, and it is probable that this undergoes important assimilative changes in its course through the liver.

(4) *The erectile tissues.*—These tissues are remarkable for the great variations in bulk they present, owing to changes in the supply of blood to them, and to the retention of the blood in their substance, which is effected by the relaxation of the muscular tissue of these arteries, and the distension of large sinuses in the substance of the cavernous tissue of which they are chiefly composed.

The **evidences of the circulation.**—Harvey was the first to demonstrate the circulation of the blood, resting his proof on the structural characters presented by the heart and blood-vessels. It remained for Malpighi to show the minute connecting vessels, named capillaries, between the arteries and veins, and

the current of blood that traverses them. The chief evidences of the circulation are:

1. The rhythmical action of the heart, taken into consideration with the arrangement and action of its valves. The heart at each beat contracts, and may be seen (when exposed by removal of the chest walls, or in malformation in a living animal), after becoming distended, to diminish in size, become paler, and to drive the blood out of its cavities. It is possible that the effect of this action might only be to cause a to-and-fro movement of the blood, that the heart might suck in at its arterial and venous extremities, during the interval of contraction, the blood that it forced out the next moment in contraction; and this is partially true in the case of the first chamber of the heart, the right auricle, and probably also in the left auricle, for whilst each of these in contracting drives part of the blood it contains onwards into the corresponding ventricle, a part also regurgitates, in the case of the right auricle into the great veins of the neck, as the jugular and subclavian, and in the case of the left auricle towards the lungs. When the blood, however, has entered the ventricles, and the walls of their cavities contract, its backward flow is effectually prevented by the closure of the auriculo-ventricular valves; and in like manner, when the contraction of the ventricles has forced the blood they contain into the large arteries, the return of this fluid is arrested by the semilunar valves situated at their origin. But since the blood enters the vessels in successive jets and none returns, it is evident that the blood must be driven forward till it can re-enter the heart at some point behind the valves, that is, by the great veins, and hence must circulate.

2. Evidence of the circulation may be derived from observing the effects of ligature or pressure on arteries and veins respectively. If firm pressure or a

ligature be applied to an artery, the proximal part, or that part above the ligature or nearest to the heart, remains distended with blood, while the distal part, or part beyond the ligature, remains empty and flaccid, until the collateral circulation is established. If the proximal segment be pricked the blood flows in jets corresponding to the beats of the heart; but if the distal segment be opened, the blood flows slowly, feebly, and with little or no jetting movement.

If firm pressure or a ligature be applied to a vein, the distal segment becomes distended with blood, whilst the proximal, though still containing blood, is relatively flaccid; and if the blood it contains be pressed up above a valve, the part between the ligature and the valve long remains empty, only gradually filling by means of the small veins that may happen to open into it.

3. The presence of corpuscles in the blood enables the movement of this fluid to be followed in the minute vessels named capillaries, in transparent parts such as the tongue of the frog, the web of its foot, or in the tail of the tadpole, or in the mesentery of one of the higher animals, which by suitable arrangements can in the living animal be placed under the microscope. And it may then be seen that it pursues a constant direction, its course being always from the arteries through the capillaries into the veins. Ligature of the main artery or vein of the limb temporarily arrests the flow, though it may recommence when the collateral circulation is established.

4. Evidence of the circulation of the blood is derived from the rapid appearance of substances, recognisable by chemical tests, in parts of the body remote from that at which they have been introduced. Thus, a salt of baryta introduced into the femoral vein may be shown to be present in the jugular vein of the opposite side in a few seconds, long before it

could have reached this position by mere diffusion; and the more vigorous and active the circulation, the more quickly can the salt be recognised. The action of poisons points in the same direction.

5. When an artery is divided the blood flows freely in jets from the upper extremity, but only feebly and slowly from the lower opening. On the contrary, when a vein is divided blood flows freely from the distal extremity, but after the discharge of that which occupies the space between the proximal opening and the nearest valve, the escape from the proximal opening is almost wholly arrested. The mere spurting of the blood at each systole of the heart from a divided artery is not in itself sufficient evidence, since it might occur in a system of tubes into which fluid was intermittingly pumped.

The presence of valves in the veins constitutes one link in the chain of evidence, both on account of their position and arrangement. These valves all point with their free edge towards the heart; they therefore prevent any backward movement of the blood flowing through the veins. These valves are almost exclusively found where the veins are subject to the pressure of surrounding or immediately adja cent muscles. When such muscles contract, the veins are compressed, and the column of blood they contain, were it stationary, would be urged in opposite directions, and their cavities emptied; but the presence of the valves prevents the backward flow, and aids the movement in the direction towards the heart.

6. Granting that the cardiac valves act, and that a certain quantity of blood is discharged from the ventricles at each systole of the heart, a circulation must exist, since more blood traverses the heart in half an hour than is contained in the whole body, whilst nothing like this quantity of fluid is discharged

from the body by the skin and lungs and kidneys taken together.

7. Subsidiary evidence is supplied by the relative thickness and strength of the right and left ventricle in accordance with the work they have to perform in driving the blood through the greater and lesser circulations respectively.

8. The conclusion that a circulation exists may also be drawn from the consideration that the various tissues of the body undergo perpetual waste and require renewal in the performance of the various acts of life, and that some kind of circulation similar to that pointed to by other evidence, is required in order that the new material should reach the tissues and the waste products be carried away.

Mode of healing of wounds.—The exceptions to the rule that, in passing through life, cuts, wounds, and bruises are received, are so rare that recovery from such injuries is regarded as a matter of course, whilst it may easily be shown that provisions for repair are normally present, and the process itself may truly be regarded as one of a physiological nature. It has been carefully examined by many pathologists, and it may be said that the broad facts are now well known. A clean cut through the skin with a sharp instrument, if the edges are brought together and kept in apposition, rapidly heals, the parts adhering and soon becoming firmly glued together. The escape of blood may be very small; but blood, speaking generally, must be regarded as a foreign body, and by its presence interferes with and protracts the healing of wounds. When wounds are exposed to the air, a thin layer of lymph, probably derived essentially from the divided lymphatics, forms on the surface and soon hardens into a greyish crust. If a section be made through this crust and the adjoining tissue, it will be found that the crust is composed

at first of a semifluid or gelatinous substance, having a large number of small, irregularly-shaped corpuscles, resembling those of the lymph embedded in it. These corpuscles are probably those of the lymph, but very soon after this layer is effused, its corpuscles become granular and undergo fatty degeneration, and they, together with the albuminous fluid in which they lie, are to a greater or less extent absorbed. Examination of the adjoining tissue, in the course of forty-eight hours after the infliction of the wound, shows that it also is infiltrated with corpuscles; but these are larger and multinucleated, and appear to have a different origin from those contained in the layer of plasma exuded on the surface of the wound. They are believed to proceed from the proliferation of connective tissue or endothelial cells, which everywhere line the lymphatic spaces. The new cells become elongated and fusiform, and the periplast of each cell becomes converted into a fibrilla of fibrous tissue, whilst the nucleus remains *in situ* as the connective tissue corpuscles. Thus the fibrous part of the cicatrix is formed. Some tissues, like muscle, appear to be incapable of regeneration when divided, and union always takes place in them by connective tissue. In nerves, on the other hand, though apparently equally highly organised, perfect restoration of structure and function may occur.

THE LYMPH AND LYMPHATICS.

A system of tubes is widely distributed through the body, which, commencing sometimes in intercommunicating stellate spaces, sometimes by free blind extremities, and sometimes by channels surrounding blood-vessels, at length, after traversing one or more glands, terminates by two large vessels that open at the points of junction of the jugular and subclavian veins. These tubes contain lymph, which is a transparent, slightly yellow fluid, of

sp. gr. 1027. It closely resembles the liquor sanguinis of the blood, containing about 5 per cent. of albumin and 1 per cent. of salts, with a minute proportion of fat and of fibrin. It appears to be derived from the blood itself, and to be the surplus material that has traversed the walls of the blood-vessels to supply the tissues, which, in some parts, as the cornea, altogether obtain their nourishment from it. It thus acts as a drainage system. But it probably, also, contains products of disintegration, which, moreover, are not so far destroyed as to be incapable of further utility in the system, and hence, after being worked up in the glands and entering the blood, can again be made serviceable in the economy.

The **chyle.**—The lymphatics that commence in the villi of the intestine, and form the system of chyle vessels or lacteals, play an important part in absorption, and the fluid they contain, here named *chyle*, presents a whitish aspect from the molecules of fat that it contains after ordinary food, and is of great importance in nutrition. The lymph traversing the rootlets of the system has only a feeble power of coagulation, and presents few corpuscles; but after passing through the glands, and especially after it has gained entrance into the thoracic duct, it acquires the power of coagulating with tolerable firmness into a gelatinous clot, and it contains numerous corpuscles, some of which appear to be in process of development into coloured blood corpuscles. (*See* "Histology," pp. 84—93.)

Movement of the lymph.—In some of the lower animals, as the eel and frog, contractile cavities (lymph hearts) which beat rhythmically, effect the movement of the lymph and drive it through the vessels; but none such are known to exist in man, though the muscular coat of the lymphatics may exert a feeble propulsive action. The movement of the fluid in the lymph spaces and tubes is effected primarily by the pressure under which the blood is driven by the

heart, but partly, also, by the pressure exerted by the muscles when in contraction, aided by the valves distributed through the system, which are especially numerous in the superficial vessels. Hence exercise, by quickening the flow of fluid, prevents the accumulation of waste products in the tissues, and promotes their healthy nutrition. There is, also, a suction influence exerted at the point where the thoracic duct opens into the junction of the subclavian and jugular veins, which is occasioned by the swift flow of venous blood over the orifice of the duct. A slight additional force may be derived from the act of inspiration. The rapidity of the flow of the lymph is about 4 mm. per second, and the pressure of the lymph against the walls of the larger vessels is about 11 mm. Hg.; but it probably undergoes great variations, M. Colin obtaining from a lymphatic in the neck of a horse, 2 mm. in diameter, sixty grammes of lymph per hour when the animal was in repose, and from the same lymphatic when mastication and movements of the neck were being performed, 100 or even 110 grammes per hour.

The **lymphatic system** has close relations with the cavities of the serous membranes, with which it communicates by means of minute orifices or stomata. Milk or other bland fluid injected into the serous cavities is quickly absorbed into the lymphatic system.

CHAPTER V.

RESPIRATION.

Object and nature of respiration.— The object of respiration is the introduction of oxygen into the system, which is accomplished by the exposure of the blood in an extremely thin layer in

the lungs to a current of atmospheric air. Coincidentally, and as a secondary process, carbonic acid gas, with which the blood coming to the lungs is charged, is eliminated. The surface presented by the capillaries of the lungs has been estimated to be about 150 square meters, and the blood at any one moment present in the lungs to be about two litres, whilst in the course of twenty-four hours about 20,000 litres traverse the capillaries, the blood corpuscles passing in single file, and being exposed to air on both surfaces. The absorption of oxygen is due to two circumstances. First, to the absorption of oxygen under the partial pressure of that gas at which the blood stands; and secondly, to the affinity of hæmoglobin for oxygen. The red corpuscles, which are chiefly composed of hæmoglobin, are the principal oxygen carriers. The elimination of carbonic acid, on the other hand, is due to the circumstance that the alkaline salts of the blood, charged with this gas, are placed under conditions favourable to its diffusion, and cease to retain it. The carbonic acid gas is generated in the tissues and enters the blood under pressure, but in the capillaries of the lungs the partial pressure of the gas is greatly reduced, and it accordingly escapes. That process by which the oxygen carried by the blood corpuscles through the systemic vessels to the tissues, leaves the blood to unite with the constituents of those tissues, and by which the carbonic acid gas with which the tissues are surcharged leaves them and enters the blood, is termed *internal respiration.* That process by which the blood traversing the lungs absorbs oxygen from the air and yields up carbonic acid gas to it is termed *external respiration.* The skin plays a subordinate part in external respiration.

The **respiratory movements.**—The ingress and egress of air is effected rhythmically by the alternate enlargement and contraction of the cavity of

the chest, which takes place in the adult from 16 to 24 times per minute, each complete act occupying therefore about three seconds. At birth the number of respirations is about 40 per minute, becoming less year by year. The proportion of respiratory acts to the cardiac beats is about two to nine or ten. The act of enlargement of the chest cavity is termed *inspiration;* that by which its capacity is diminished *expiration.*

The **act of inspiration.**—In inspiration the thoracic walls are drawn apart in all directions, and the cavity of the chest is enlarged by muscular action. A tendency to a vacuum is produced; air immediately rushes through the trachea into the lungs, which passively expand to fill the enlarging space, and to equalise the pressure within and without the chest. If the mouth and nostrils be closed no effort will expand the chest, because the pressure of the atmosphere on the outside of the chest is greater than the muscles can overcome; but if the muscles were of such strength that they could overcome the atmospheric pressure, then the ribs, with the parietal layer of the pleura, would separate from the lungs covered with the visceral layer of the pleura, and a vacuum would be formed between the two layers of the pleura, which, however, would soon be filled by the distension of the lungs with blood, for under normal conditions both blood and air are drawn to the lungs in inspiration; but air, being much lighter and more mobile, naturally enters in larger quantities. The lungs are always under negative pressure, since they collapse when an opening is made into the pleura. The muscles engaged in effecting inspiration, and especially forced inspiration, are numerous, but one stands out pre-eminent amongst the rest, and probably almost acts alone in tranquil inspiration—*the diaphragm.* This muscle when at rest forms an arch, on the upper convex surface of which the heart and lungs rest. In

contraction the lateral portions of the arch become flattened, the cavity of the chest is correspondingly enlarged, and the lungs descend. The central tendon, on which the heart rests, and through which the inferior vena cava passes, remains comparatively stationary, as is conclusively shown by the slight variation in the region over which the apex beat of the heart can be felt in inspiration and expiration respectively. For since the pericardium is firmly attached to the central tendon, the heart must necessarily follow the movements of that tendon, and as its situation remains nearly unaltered, the position of the tendon can be but little disturbed. The importance of the diaphragm is shown by the fact that if both phrenics, which are its motor nerves, be cut, death results, the other muscles collectively being unable to maintain respiration effectively. The next most important group of muscles acting in tranquil inspiration are the *scaleni*, which fix the first and second ribs and the *external intercostals*, the fibres of which run downwards and forwards, and which, taking the first rib as a fixed point, act successively on the ribs below, pulling them outwards and upwards, and thus enlarge the intercostal spaces. The *levatores costarum* are also believed to act in tranquil inspiration.

The **act of expiration.**—Tranquil expiration is effected only to a trifling extent by muscular action, and results from the elasticity of the lungs and walls of the chest and of the abdominal viscera.

Forced respiration.—When from violent muscular effort the right heart and lungs become surcharged with blood, or when the respiratory passages are constricted, or when the respiratory centres are supplied with blood containing a deficiency of oxygen and an excess of carbonic acid gas, difficulty of respiration or *dyspnœa* is induced, and *forced efforts* of inspiration and expiration are made, in which many muscles take

part. The following table, taken from Landois, shows the muscles engaged in tranquil and in forced respiration, and gives also their nerve supply.

A. INSPIRATION.

I. In Tranquil Inspiration the Muscles acting are:

1. The diaphragm (*Nervus phrenicus*).
2. The three scaleni (*Rami muscul. plex. cervicalis et brachialis*).
3. The levatores costarum (*Ram. poster. nerv. dorsalium*).
4. The external intercostal muscles (*Nerv. intercostales*).

II. In Forced Inspiration the Active Muscles are:

a. Muscles of the Trunk.

1. The sterno-mastoid (*Ramus externus nervi accessorii*).
2. The trapezius (*Ram. ext. nerv. accessorii et ram. musculares plex. cervicalis*).
3. The pectoralis minor (*Nn. thoracici anteriores*).
4. The serratus posticus superior (*N. dorsalis scapulæ*).
5. The rhomboidei (*N. dorsalis scapulæ*).
6. The extensors of the vertebral column (*Ram. post. nervorum dorsalium*).
7. [The serratus anticus major (*N. thoracicus longus*).] ?

b. Muscles of the Larynx.

1. The sterno-hyoid (*Ram. descendens hypoglossi*).
2. The sterno-thyroid (*Ram. descendens hypoglossi*).
3. The crico-arytænoïdeus posticus (*Nerv. laryngeus inferior vagi*).
4. The thyro-arytænoid (*Nerv. laryngeus inferior vagi*).

c. Muscles of the Face.

1. The dilatatores narium, anterior and posterior (*N. facialis*).
2. The levator alæ nasi (*N. facialis*).
3. The expanders of the mouth and nares (*N. facialis*).

d. Muscles of the Pharynx.

1. The levator veli palatini (*N. facialis*).
2. The azygos uvulæ (*N. facialis*).

B. EXPIRATION.

1. Tranquil Expiration is effected essentially

By the elasticity of the lungs, costal cartilages, and abdominal muscles, and by the weight of the chest walls.

2. In Forced Expiration the Muscles acting are

1. The abdominal muscles (*Nn. abdominis interni s. anteriores e nervis intercostales*).
2. The triangularis sterni (*Nn. intercostales*).
3. The serratus posticus inferior (*Ram. ext. nerv. dorsalium*).
4. The quadratus lumborum (*Ram. musculares e plex. lumbale*).
5. The intercostales interni so far as they lie between the bony ribs, and the infracostales (*Nn. intercostales*).

The ribs are fixed at their extremities, whilst their central curved part plays comparatively freely in the act of respiration, like the handle of a bucket. Those muscles which raise the ribs also separate them from each other, and act therefore as muscles of inspiration. Those that depress the ribs approximate them to each other, lessen the cavity of the chest, and act as muscles of expiration. In dyspnœa, as in asthma, the body is bent forwards, the hands grasp a chair back, or rest on some solid object, in order to fix the shoulders and to enable the pectorales, scaleni, sterno-mastoid, and intercostals, to act with most advantage in expanding the chest. Much discussion has been held in regard to the action of the intercostals. The points well settled are, that the external intercostals, which run downwards and forwards, and, therefore, from the less movable part of the rib above to the more movable part of the rib below, must act as elevators of the ribs, and as muscles of inspiration, providing the first rib is fixed. And in like manner, that portion of the internal intercostals which is between the costal cartilages (since the fibres run downwards and backwards, and, therefore, again from the less to the more movable part of the ribs, for the ribs are fixed at the sternum, as well as at the spine) must raise the ribs, and separate them from each other, providing the first rib is fixed. But it is conceivable that if the intercostal muscles were acting simultaneously, *per se*, and not in concert with other muscles, they would bring the ribs together, contract the chest, and act as muscles of

expiration. Different instruments have been employed to measure the variations in the diameter of the chest at different periods of the respiratory acts; amongst them are the *thoracometer* of Sibson, the *cyrtometer* of Woillez. The absolute enlargement of the chest in the antero-posterior and transverse direction, in tranquil respiration, does not exceed half a centimetre or five mm. In forced respiration it is about three centimetres at the level of the seventh or eighth rib. The amount of the vertical enlargement of the chest, caused by the descent of the diaphragm, is not known in man, but in the horse it has been estimated to be three times greater than the increase of the transverse diameter.

Duration of the acts of respiration.—Tracings of the respiratory acts show that the act of inspiration is shorter than that of expiration in the proportion of 6 : 7 or 6 : 8. Inspiration commences with moderate rapidity, then becomes more rapid, and towards its close somewhat slower. Expiration begins with moderate rapidity, then becomes quicker, and towards the close of the act very slow. There is no pause between expiration and inspiration.

Types of respiration. 1. *Abdominal type.*—In the adult male, and in infants during the first three years of life, the diaphragm is usually the chief muscle employed in tranquil inspiration, and its descent causes the viscera to press on the abdominal walls, and the belly rises and falls with each act of respiration. This type of respiration may also be observed in the horse, cat, and rabbit.

2. *Inferior costal type.*—This type occurs in many adult males, and especially in boys after the third year. The diaphragm acts, but the abdominal walls move but slightly, and the expansion of the chest is chiefly affected by the raising and separation of the ribs from the seventh upwards. It is seen in the dog.

3. *Superior costal type.*—In this type the clavicles, upper part of the sternum, and the upper ribs, play freely, whilst the lower part of the chest and the abdominal walls are almost motionless. It is characteristic of the female, enabling her to respire freely when the movements of the diaphragm and lower ribs are interfered with by the great enlargement of the uterus in pregnancy.

In infancy, when the child sucks, respiration is carried on exclusively through the nose, and a simple catarrh, by causing tumefaction of the pituitary mucous membrane, may cause death by asphyxia or by inanition; by the child being unable to breathe on the one hand, or take nourishment on the other.

Capacity of the chest.—The volume of air contained in the lungs of a healthy adult male after the fullest possible inspiration, is about 5,650 cubic centimetres, and it has been found convenient to divide this into four parts.

(1) *Tidal or breathing air,* which is that volume inspired and expired with each act of respiration.

(2) *Complemental air;* or that volume of air which can be inspired after an ordinary inspiration.

(3) *Reserve, or supplemental air,* or that volume of air which can be expired after an ordinary expiration.

(4) *Residual air.*—That volume which remains in the lungs after the fullest possible expiration.

These several volumes may be expressed in cubic centimetres as follows:

1.	Tidal air . . .	500	cubic centimetres.
2.	Complemental air . .	1,670	„ „
3.	Reserve air . .	1,600	„ „
4.	Residual air . .	1,880	„ „

The first three of these volumes can be taken into, or expelled from, the chest at will, and have been collectively termed the *vital capacity.* The average vital capacity of a man of 5 ft. 8 ins. is 3,770 cubic centimetres.

The vital capacity is modified (1) by height, (2) by position, (3) by weight, (4) by age, and (5) by disease.

(1) In regard to height, every inch of stature from five to six feet enables the subject to expire eight additional cubic inches by a forced expiration after a full inspiration.

(2) In regard to position, it is found that more air can be inspired in the erect than in the recumbent position, because the movement of the chest walls is more free in the erect posture.

(3) Speaking generally, it may be said that with increased weight, within moderate limits, there is increased vital capacity.

(4) In regard to age, the vital capacity increases from 15 to 35 years, and from 35 to 65 it decreases.

(5) All abdominal and thoracic diseases, as tumours, abscesses, phthisis, diminish the vital capacity.

Renewal of the air in the lungs.—At each inspiration about 500 cc. of pure air penetrate into the lungs. Of these 500 cc., about 330 cc. remain in the lung, and mix by diffusion with the vitiated air there present. The first portions of the air expelled in expiration have not penetrated into the lung. These numbers have been obtained by Gréhant, who made an inspiration in pure hydrogen gas, and introduced in this way 500 cc. of this gas into his lungs. In the immediately succeeding expiration he found 170 cc. H mixed with 330 cc. of air. He then continued to respire air, and found that the three following expirations contained respectively 80·5, 41, and 40·8 cc. of H. Gréhant applies the term *coefficient of pulmonary ventilation* to the number obtained by dividing the quantity of pure air introduced into the lungs in one inspiration (330 cc.), by the quantity of vitiated air contained in the lungs before this inspiration (= Reserve + residual air). This number is about 0·1, that is to say, that the mass of vitiated air in the

lungs mixes at each inspiration with about $\frac{1}{10}$ of its volume of pure air. The air in the lungs may therefore be considered as completely renovated in from 8 to 10 respiratory acts.

Influence of the vagi on respiration.—If the vagus be divided in the cervical region on one side, and the central extremity be stimulated with a series of induction shocks, the respiratory movements are found to be increased in rapidity, and with strong stimulation the diaphragm may be thrown into a state of tetanus. These effects seem to show that there are *fibres ministering to inspiration* in the trunk of the vagus, running in a centripetal direction. These fibres are stimulated when the act of expiration is completed, possibly to some extent by the mere mechanical action of the walls of the alveoli falling together; for if the chest walls be perforated, and air be allowed to enter the pleural cavity, the collapse of the lungs is soon followed by violent spasmodic contractions of the diaphragm, which, however, only occur providing the vagi are intact. There is evidence, however, that the vagi contain also *fibres ministering to expiration*, since under certain conditions, as in rabbits under the influence of a dose of chloral, excitation of the central end of the vagus is invariably followed by an arrest of respiration in expiration. (Fredericq). These fibres are excited each time that the lungs are mechanically distended, either by inspiration or by artificial inflation of the lungs. Inspiration, therefore, induces expiration, and expiration calls forth an inspiratory act, and thus the regular sequence of the respiratory acts is provided for. The effect of insufflation of the lung is well shown in the following tracing by Frédéricq.

The superior laryngeal nerve contains a large number of the fibres capable, when stimulated, of exciting expiration, the slightest irritation of the

glottis, which is supplied with sensory filaments by this nerve, causing expiration. Section of both vagi

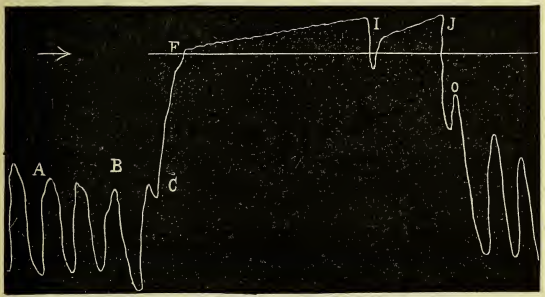


Fig. 9a.—Showing the arrest of the respiratory act and the prolongation of the expiratory act, caused by insufflation of the Lungs. A to B, normal respiratory tracing; at C insufflation was performed; at F the trachea was closed in order to keep the lungs distended; from F to I, expiration; at I the first inspiration was made; at O the tube was opened. (*After* Frédéricq.)

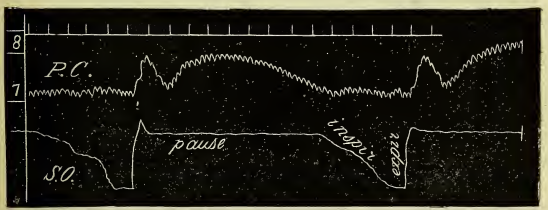


Fig. 9b.—SO, Tracing of the respiration taken with the œsophagus sound in the Dog, after the section of both Vagi. PC, pressure in the carotid. Uppermost line showing seconds. (*After* Frédéricq.)

materially alters the rhythm of respiration. The movements becoming slower and deeper, long pauses being succeeded by an act of full inspiration, followed by an act of expiration.

Other nerves beside the vagi may conduct centripetal impulses or stimuli to the respiratory centres. The most important of these is undoubtedly the fifth, and its influence is familiar in the deep inspiration that occurs when the face is suddenly exposed to cold, as by being flipped with a cold wet cloth, or drenched with cold water; and the same effect is produced by the application of cold to other sensory nerves.

The **respiratory centres.**—The centres which preside over the acts of respiration occupy a symmetrical position on either side of the median line in the lower part of the medulla oblongata, a little above the origin of the vagi, and opposite the interspace between the occipital bone and atlas. It is believed that there are two on each side, one regulating the movements of inspiration, the other of expiration. The evidence demonstrating that the centres occupy this position is that the spinal cord may be divided from below, and the brain may be removed by successive slices from above, without arresting respiration, until this spot is injured, when respiration at once ceases; whilst, if this region is damaged alone, though the rest of the nervous system is intact, the respiratory acts are at once and permanently arrested, and death promptly follows. Hence this region of the medulla has been named the *nœud vital.*

The respiratory centres can be excited to act both by direct and by reflex stimulation. Their excitability by direct stimulation is shown by their increased action when an electrical current is transmitted through them. Cold, on the other hand, depresses their activity. When all *sensory* nerves by which the centres might be stimulated are divided, respiratory movements, though irregular in rhythm and depth, still continue, and it seems probable that these movements are then due to the circulation through the medulla of blood deficient in oxygen, and

containing an excess of CO_2. It has been shown by experiment, that after section of the vagi, which prevents the passage of stimuli from the lungs, deficiency of oxygen acts as an excitor of the inspiratory centre, whilst excess of CO_2 stimulates the expiratory centre.

In tranquil respiration, or *eupnœa*, it is probable that the defective supply of oxygen and excess of CO_2 in the blood circulating through the capillaries of the lungs, stimulate the peripheric terminations of the vagus. The stimulus is conveyed by this nerve to the respiratory centres, which at once respond, and liberate impulses, which, travelling down the spinal cord, pass along the motor nerves supplying the diaphragm and intercostal muscles, and inspiration follows. The entrance and absorption by the blood, of oxygen, then temporarily leads to quiescence of the centres and relaxation of the muscles, and a fresh inspiration is only made when the deficiency of oxygen rises to a certain amount.

If by rapid and deep breathing a large proportion of oxygen is introduced into the system, the need for the acts of respiration is less felt ; no motor impulses emanate from the respiratory centres, and the condition termed *apnœa* is established. On the contrary, if the supply of oxygen fail, and CO_2 accumulates in the blood, violent muscular efforts, both of expiration and of inspiration, are made, in which almost every muscle in the body takes a part, and the subject is said to suffer from *dyspnœa*.

In all violent efforts, a deep inspiration is instinctively taken, and the glottis closed by the arytænoid and lateral crico-arytænoid muscles, the object of which is to fix the chest, and to afford a *point d'appui* to the upper limbs.

Sounds of respiration.—If the ear be applied to the uncovered chest of a person breathing tranquilly, a soft blowing murmur is heard during

inspiration, over the whole of those regions beneath which the lungs are situated. This sound, named the *vesicular murmur*, is also audible during expiration. It is caused by the distension and separation of the walls of the air vesicles and smaller channels leading to them, and to the friction of the air over the numerous points of division of the air tubes. If the ear be placed over the trachea in front, or the larger bronchi at the back, on either side of the vertebral column, a louder and rougher sound is heard, termed the *bronchial murmur*. It is audible both in inspiration and in expiration.

Percussion sounds of the chest.—When the chest is lightly tapped with the finger, or with a pleximeter, the regions beneath which the lung is situated are resonant, or yield a hollow sound, whilst the part over the heart is dull. The apices of the lungs reach an inch or more above the clavicle in front, and nearly up to the level of the spinous process of the seventh cervical vetebra behind. The lower border of the lung, in *moderate expiration*, commences on the *right* side, at the border of the sternum opposite the attachment of the sixth rib, then runs nearly parallel with the upper border of the sixth rib, descends a little in the axillary region to the border of the seventh rib, and posteriorly is level with the tenth rib. The relations are the same on the *left* side, except in the region near the sternum corresponding to the fourth, fifth, and sixth ribs, where the right ventricle of the heart is in immediate relation with the ribs. *In full inspiration*, the superior borders of the lungs descend below the seventh rib in front and laterally, and as low as the eleventh rib posteriorly, and on the left side the lung advances considerably in front of the heart, leaving only a small area uncovered. In full expiration, on the other hand, the lower border of the lungs rises nearly the breadth of an intercostal

space, and on the left side a large part of the ventricle is uncovered.

Variations of pressure in the air passages.—If a manometer be connected with an opening in the trachea, whilst the respiratory acts are otherwise normally performed, it is found that, with each inspiration, a negative pressure equal to 3 mm. of mercury is exerted, whilst during expiration there is a corresponding positive pressure. If the manometer tube be inserted into one nostril, and tranquil respiration carried on through the other, with closed mouth, the inspiratory negative pressure is 1 mm. of mercury, the positive expiratory pressure is from 2 to 3 mm. When all the inspiratory or expiratory muscles are brought into play, the pressures, both negative and positive, are greatly increased. Thus the inspiratory muscles of a medium-sized adult male can exert a negative pressure capable of raising a column of mercury 75 mm. high, whilst the expiratory muscles, aided by the elasticity of the chest walls and lungs, can exert positive pressure capable of raising a column of mercury 100 mm. in height. It may, indeed, under special circumstances, attain still greater height, as in the experiment sometimes termed Müller's experiment. This consists in closing the glottis after a forced expiration, and then making a violent inspiratory effort. The negative pressure thus induced may attain such a height that the auricles, distended by the inspiratory effort, no longer transmit their blood into the ventricles. The pulse-waves caused by the contractions of the left ventricle diminish in height, and the pulse may now be completely arrested. As a result of this, the vessels of the systemic circulation are rendered anæmic, whilst those of the pulmonary circulation become hyperæmic.

In the experiment, sometimes, but erroneously, termed Valsalva's experiment, the pleural pressure

may, on the contrary, be greatly augmented. In this the glottis is closed after a full inspiration; a violent expiratory effort is then made, and the positive pressure has been observed of 250 mm. of mercury. Under these conditions the great veins can no longer discharge their contents into the chest; the blood accumulates therefore in the systemic vessels, the lungs become empty, and after a short time, the left heart receiving no blood, the pulse becomes imperceptible. These experiments are not free from danger (Frédéricq).

Absorption of gases by fluids.—Gases are absorbed to a greater or less extent by water and other fluids, the amount absorbed being dependent (1) on pressure, (2) on temperature, and (3) on affinity. The weight that is taken up of any gas by the same liquid at a given temperature is proportional to the *pressure*, or, which is the same thing, the volume of the gas dissolved is at all pressures the same. Hence it is found that when the pressure is doubled the weight of dissolved gas is also doubled. *Temperature* is of great importance, since the quantity of gas absorbed decreases with the temperature. Thus at 0° C. and 1 m. pressure, water will absorb 1·79 vol. of CO_2, but at 15° C. it will only absorb 1 vol. The quantity of gas which a liquid can dissolve is independent of the nature and of the quantity of other gases which it may already hold in solution. If a fluid is exposed to a mixture of several gases, the pressure on its surface is equal to the sum of the pressures of the several gases, but each gas only exerts the same pressure that it would do if it occupied the whole space above the fluid, and in a mixture this is called its "partial pressure." Thus oxygen forms one-fifth of any quantity of air, and water exposed to air absorbs only such a quantity of oxygen as it would do if the atmosphere were entirely formed of this gas under a pressure equal to one-fifth that of the atmosphere. Thus,

since the pressure of the atmosphere is 760 mm. at the level of the sea,

the pressure of oxygen $= \frac{760 \times 20{\cdot}8}{100} = 158$ mm.;

the pressure of the nitrogen $= \frac{760 \times 79{\cdot}2}{100} = 601$ mm.;

the pressure of the $CO_2 = \frac{760 \times 0{\cdot}00025}{100} = 0{\cdot}052$ mm.

The numbers 158, 601, 0·052 represent therefore the partial pressure of the several gases mentioned. The partial pressure of oxygen in the air vesicles during calm expiration is found to sink to 117 mm., and in a deep inspiration is 130 mm., whilst the partial pressure of CO_2 rises in tranquil respiration to 31·5 mm., and in deep expiration to 66·4 mm.

Inasmuch as the relative quantity of oxygen contained in the air occupying the alveoli of the lung is, owing to its absorption by the blood, diminished to about 16 per cent., the partial pressure is reduced to $\frac{16}{100}$ or to about $\frac{1}{6}$ of 760 mm., or 126 mm. of mercury. But if we inquire what the tension of the oxygen in the venous blood contained in the capillaries of the lungs is, we are met with the difficulty that whilst no doubt a part of the oxygen is merely in solution, the major portion is in direct chemical union with the hæmoglobin. The absolute quantity of oxygen in the pulmonary venous blood is about 14 per cent., and the quantity of the uncombined oxygen has been ascertained by placing different portions of the same venous blood in contact with different gaseous mixtures more or less rich in oxygen, and of known composition. If the tension of the oxygen in the blood is greater than that of the oxygen in the gaseous mixture, it will yield up the excess till an equilibrium is established; and on the other hand, if the tension is greater the blood will absorb a certain amount of oxygen. By making a series of experiments in this

way, Pflüger has shown that a state of equilibrium is attained when the quantity of oxygen contained in the gaseous mixture is 2·9 per cent., *i.e.* about $\frac{1}{33}$, representing a partial pressure capable of supporting a column of mercury of about 23 mm. in height. Blood exposed to such a mixture neither absorbs nor gives up oxygen.

Chemistry of respiration.—As the chemical changes in respiration take place between the gases contained in the air and the blood, it is requisite in the first place to ascertain the composition of the gases which can be extracted without chemical decomposition from these two fluids respectively.

The composition of pure dry air is well known. It contains in every 100 volumes 21 volumes of oxygen gas and 79 volumes of nitrogen gas, or, if estimated by weight, in any 100 grains there are 23 grains of oxygen and 77 grains of nitrogen. It further contains four parts of carbon dioxide in every 10,000 volumes. Its composition is constant up to a height of 14,000 feet. In crowded theatres the quantity of oxygen may fall nearly 1 per cent., and the amount of carbon dioxide may rise to 70 parts in 10,000, and on both accounts the air becomes distinctly prejudicial to health. Ordinary air contains in addition a variable quantity of watery vapour. If saturated, a cubic metre of air takes up at 10° C. 9·362 grains of aqueous vapour. The higher the temperature the more water can it contain, the lower the temperature, the less. Thus, 1 cub. met. of air at 35° C. is saturated with 39·25 grains of aqueous vapour, whereas at 0° C. it can hold only 4·87 grains. Air is rarely saturated with aqueous vapour, and the quantity rarely falls below $\frac{1}{10}$ of the saturating quantity. Lastly, the air contains a trace of ammonia.

The **gases of the blood.**—The most reliable observations that have been made on this point are

those of Pflüger, who found that nearly 60 volumes of gases could be extracted from 100 volumes of *arterial* blood immediately after it had been withdrawn from the body. These gases consisted of oxygen 22·2 vol., carbon dioxide 34·3 vol., and N_2 1·8 volumes. *Venous* blood, in becoming changed into arterial, gains from 4 to 20 per cent. of oxygen by volume, and loses from 3 to 13 per cent. of carbon dioxide. The arterial blood returning from the lungs is probably saturated, so far as the hæmoglobin is concerned, with oxygen; that is to say, the hæmoglobin has taken up as much oxygen as it is possible for it to combine with, since, as just stated, it has been demonstrated by experiment that, to effect this, a partial pressure of oxygen amounting to 3 per cent. is all that is required; but the plasma is, according to Frédéricq, far from being saturated with oxygen; for the laws of diffusion require that the air in the pulmonary alveoli should surrender oxygen to the blood until an equilibrium of tension is established. If the arterial blood, therefore, which is returning from the lung, were saturated with oxygen, it ought to present a tension equal to that which this gas presents in the alveoli of the lungs, that is, about 16 per cent. of an atmosphere. But the actual partial pressure of the oxygen in the blood returning from the lungs, as shown by the aerotonometer of Pflüger, does not pass the limit of 10 per cent., and may be as low as 3·9 per cent. It is clear, therefore, that an equilibrium of tension between the oxygen in the air and blood is far from being attained in the lung. It may be taken as a fact certainly established, that the absolute quantity of oxygen contained in the arterial blood of the same animal is undergoing constant variation in amount according to the requirements of the system. The tension of CO_2 in the venous blood entering the lung has been found to vary between 3·81 per cent. and 5·4 per cent. of an atmosphere; whilst

the tension of CO_2 in the air entering the lung is scarcely appreciable. Perfect equilibrium of tension in regard to CO_2, between the CO_2 of the air in the alveoli and in the blood, is effected in the lung, as is shown by the fact that the last portions of air escaping from the lung in expiration and arterial blood contain about equal proportions of CO_2. The absolute amount of CO_2 contained in the blood may vary within wide limits, which is due to the circumstance that the larger part of this gas exists in the form of dissociable combination, and a slight diminution of tension is sufficient to effect the decomposition of a notable quantity of these compounds. In the mere act of spontaneous coagulation the alkalinity of the blood rapidly diminishes, and the tension of the CO_2 rises considerably, attaining as high a degree as 8 per cent. of an atmosphere.

Changes in the air that has been once breathed.—(1) The proportion of carbonic dioxide (CO_2) is increased to 4·3 per cent., so that after a single act of tranquil respiration, air, which previously only contained four parts in 10,000, now contains on an average 430 parts in 10,000 volumes.

(2) The proportion of oxygen gas is diminished on an average about 4·8 per cent., so that whilst ordinary air contains 21 per cent. of oxygen, air that has been once breathed contains only 16·2 per cent. The excess of oxygen taken up by the blood over the oxygen discharged as carbonic dioxide is probably applied to the oxydation of other constituents of the body, as sulphur and phosphorus.

(3) A small quantity of nitrogen is generally added to it.

(4) It is saturated with watery vapour. One cubic metre of expired air at 37° C. containing about 42 grammes of watery vapour.

(5) Its temperature is increased, usually, in tem-

perate climates, rising to 36·3° C., but several degrees lower if the air inspired be very cold, and a degree or two higher if hot.

(6) Its volume is increased, the slight decrease due to excess of O absorbed over CO_2 eliminated * being more than compensated by expansion from heat and addition of watery vapour.

(7) There is an addition to it of small quantities of ammonia, hydrogen, and marsh gas.

(8) It is freed from all germs and particles of dust.

The absolute quantity of oxygen gas absorbed into the system per diem by the lungs is about 750 grammes, of carbonic dioxide eliminated about 900 grammes, of water eliminated about 450 grammes.

Vierordt has shown that the quantity of O consumed per hour by man for each kilogram of his weight, at 0° C. and 760 mm. pressure, is about 300 cubic centimetres. The quantity, however, varies within very wide limits in other animals. Thus, whilst in the calf, pig, and sheep it is about the same as in man, in the case of the rabbit, instead of 300, it is 687 cub. cent. ; in the dog, 900 cc. ; in the guinea-pig, 1,110 ; in small birds, from 9,000 to 10,000. In animals with slower circulation and less active powers it is much smaller ; thus, in the lizard it is 134 ; in the crab, 107 ; in the earthworm, 70·8 ; and in the leech, 22. It is interesting to notice that when the vital powers are in abeyance amongst the higher animals, the quantity of oxygen they require is immediately reduced ; thus, in the case of the marmot the amount falls in *hybernation* to the very low number of 30 cc.

When the tension of CO_2 increases moderately in atmospheric air, reaching to 3, 4, or 5 per cent., the

* Equal volumes of O and of CO_2 contain equal quantities of oxygen gas.

tension of the gas increases to a corresponding extent in the organism, until a new equilibrium of tension is established between the air in the alveoli and the blood in the lung; the excess of CO_2 acts as an excitant on the respiratory nervous centres in the medulla oblongata, induces dyspnœa, and increases the intensity of the interstitial combustions. The quantity of O consumed increases (Frédéricq). CO^2 does not prove fatal until its partial pressure exceeds 20 per cent. of an atmosphere. It then acts as a narcotic poison, and considerably diminishes the intensity of the chemical phenomena of respiration.

Many circumstances modify the quantity of carbonic acid eliminated from the system. Everything which tends to increase the quantity of oxygen entering the system, or the quantity of readily oxydisable materials in the body, or which renders the oxydising process more active, will increase the elimination of carbon dioxide. Thus it is greatly increased by exercise, by food, and by exposure to cold within moderate limits. It is relatively larger in children than in adults, in men than in women, in persons of a vigorous constitution than in the languid and phlegmatic. It is also modified by certain physiological changes, as by the frequency and depth of the inspiratory acts, which, when either deeper, or more frequent with the same depth, cause increased elimination of carbon dioxide.

Muscular exertion is without doubt the condition that exercises the greatest influence on the production and discharge of carbon dioxide, and it has been estimated that if a person breathing tranquilly discharges seven or eight ounces of carbon per diem in the form of carbon, the quantity would be more than doubled with severe exertion. Under these circumstances, the respiratory quotient approaches unity, the quantity of CO_2 eliminated and of O absorbed being nearly equal.

The increase in the quantity of O taken into the system is perceptible for some minutes in the period of repose that follows muscular exertion.

The **mode of combination of carbon dioxide in the blood.**—It can be easily shown that part of the carbon dioxide contained in the blood is in combination with the coloured corpuscles, and another part with the plasma, and the combination with the plasma is firmer than with the corpuscles, but it has not been quite certainly determined in what state of combination it really exists. It is probably in the form of sodium bicarbonate, which is chiefly contained in the plasma. Experiment has shown that whilst water at 0° C. and at ordinary pressure will take up about its own volume of CO_2, blood absorbs about $2\frac{1}{2}$ times its volume. Mere exposure to a vacuum will extract the dissolved CO_2, and dissociate almost the whole of that combined with the sodium bicarbonate; and since in presence of bodies playing the part of a feeble acid, such as the proteids and especially oxyhæmoglobin, even sodium carbonate will undergo decomposition, it follows that almost the whole of the CO_2 contained in blood can be extracted by placing it in a receiver and exhausting the air. The tension of CO_2 in the blood is hence more easily ascertained than that of the oxygen, and it has been found that its tension, or partial pressure, in pulmonary venous blood varies from 3·81 per cent. to 5·4 per cent. of an atmosphere, and it is as nearly as possible identical with the tension of the carbonic acid in the alveoli of the lungs. In arterial blood the tension of CO_2 is about 2·8 per cent. of one atmosphere, and although the difference between the tension of the gas in venous and in arterial blood is comparatively small, yet the absolute quantity contained in a given volume is much greater in one case than in the other, because, as already stated, the CO_2 is

contained in the blood in the form of easily decomposed compounds.

Effects of variation in the pressure of the air on respiration.—Man lives at the bottom of a great aerial ocean, the depth of which is about fifty miles, and which, though so light, exercises an enormous pressure on the surface of his body, a pressure that, at fifteen pounds to the square inch, has been calculated to amount to thirty or forty thousand pounds, according to the extent of surface presented by the skin; but in ascending lofty mountains, or in balloon ascents, when a height of nearly thirty thousand feet has been attained, the pressure of the air is greatly diminished, and with it the partial pressure of the oxygen. If the change is effected slowly the system accommodates itself to the altered condition, and no ill effects are experienced; but if the change from air of ordinary density to air that is greatly rarefied occurs suddenly, remarkable effects are observed, which, in the case of mountain climbing, are known as the *mal de montagne*, and which are equally noticeable in balloon ascents. In the former case they are intensified by the muscular exertion which is put forth in the ascent, whilst in the latter case the suddenness of the change seems to induce the same symptoms.

These are: 1. Congestion of capillaries of the skin and free surfaces of the mucous membranes, owing to diminished pressure, which may culminate in hæmorrhage, and certainly leads to sweating and free mucous secretion. 2. The resistance to the passage of the blood through the capillaries being diminished, the cardiac beats become more frequent, and dyspnœa is experienced, and the respirations become deeper and irregular as well as more frequent. 3. The insufficient supply of oxygen and imperfect elimination of CO_2 induce extraordinary muscular weakness, the slightest exertion causing exhaustion. Hence, again, in part,

the dyspnœa and sense of constriction about the chest. 4. The vagal centres are stimulated by the insufficiency of O, and vomiting may occur; and 5. The blood being drawn from the internal organs to the surface, the brain is imperfectly supplied with oxygen, and faintness results, noises are experienced in the ears, obscurations or sparks appear before the eyes, with other symptoms of disturbance of the functions of the nervous system, and there is diminished secretion of urine.

The greatest height yet attained has been by Glaisher, who ascended in his balloon to a height of 8,840 m., when the pressure descended to 247 mm. Hg. In Sivel and Croce-Spinelli's fatal balloon ascent the barometer fell to 262 mm. Hg, and the partial pressure of the oxygen was therefore only 52 mm., showing that it was reduced to 7 per cent. of one atmosphere. In the ascent of Mont Blanc the pressure of the air falls from 750 mm. at the sea level to 418 mm. at its summit; the oxygen is therefore reduced from 20·8 to 11·53 per cent. The brothers Schlagintweit ascended the Himalayas to a height of 6,882 m., when the pressure was 320 millimetres. It has been found by experiment that dyspnœa begins to be experienced when the proportion of oxygen in the air supplied is diminished, either by reduction of pressure or by removal of part of the gas, from 20·8 per cent., which is its normal amount, to 10 per cent.; and when it has been reduced to 3 per cent., when it has a partial pressure of 22·8 mm., and usually long before this limit is reached, death occurs; for 3 per cent. corresponds to the partial pressure at which hæmoglobin is only able to absorb oxygen with difficulty, if at all. The active functions of the nervo-muscular apparatus, no longer duly supplied with O_2, cease, and death results.

Bert found that the respiration of air artificially

reduced in pressure produced similar effects to those of mal de montagne. When placed in a chamber, the tension of the air in which was 420 millimetres, or about equal to the height of Mont Blanc, the cardiac beats rose from 60 to 84 per minute. He then made three respirations of oxygen, and the pulse immediately fell to 71. He gave up respiring oxygen and made a movement, when it at once rose to 100 to redescend to 70 after the inspiration of oxygen.

A man who ascends to such a height that the mercury stands at 15 instead of 30 inches, breathes air which, so far as the oxygen it contains is concerned, contains only half the normal amount of oxygen.

As by ascending the pressure of the air can be decreased, so by descending below the sea level it can be increased, and the amount of such increase in deep mines and in works conducted under water, as in the laying of the foundations of bridges, is sometimes considerable, amounting to as much as sixty or seventy pounds avoirdupois on the square inch. In such cases the skin has been observed to become pale, and the cutaneous perspiration to diminish. The respirations are reduced in frequency by two to four in the minute. Inspiration is accomplished with greater facility, expiration is prolonged, and a distinct pause occurs between expiration and inspiration. The capacity of the lungs augments. The urinary secretion is increased, and muscular efforts are made with more activity and energy. The heart, meeting with more resistance on account of the contraction of the cutaneous capillaries, beats more slowly, and the pulse curve is lower. There is a subjective sensation of warmth. Great care should be taken that those who are subjected to such high pressure be not suddenly exposed to air at the normal pressure, for the effect is equivalent to the application of a gigantic cupping-glass to the whole body. The blood is suddenly drawn to the surface, hæmorrhage

from the nose, ears, and mouth is likely to occur, and paralysis may result from the sudden abstraction of blood from the nerve centres. Mere exposure to an atmosphere of oxygen produces no ill effects; but if the animal be exposed to oxygen under pressure, so that the blood is made to take up about 35 per cent. of its volume of O, death occurs in convulsions.

Effects of breathing in a confined space.—The effects of breathing in a limited space differ to some extent in accordance with the size of the space. If the space be small, or only of moderate size in comparison with the animal, a large part of the oxygen is used up, and a nearly corresponding volume of CO_2 is eliminated. The fact that so much of the oxygen disappears is a clear proof that its absorption by the blood is due to chemical affinity, and is not the result of the operation of the usual laws of absorption of gases by fluids. Death results from asphyxia, due to a deficiency of oxygen, the tension of the gas descending below the limit compatible with life.

In large but confined spaces, though death results from asphyxia, it is rather due to accumulation of CO_2 than to a deficiency of oxygen; at least, the animal dies long before the oxygen is altogether exhausted. If arrangements are made by which the CO_2 is removed as fast as it is formed, the animal will live much longer than if it be allowed to breathe the same air more or less charged with CO_2 over and over again. In fact, if animals be made to breathe a mixture of half oxygen and half CO_2 death results, not because there is a deficiency of oxygen, but because there is an excess of CO_2, which is absorbed, and then acts as a poison.

In pure oxygen animals breathe quite normally, and the substitution of hydrogen gas for nitrogen may be made without in any way interfering with respiration. When, however, the tension of the O exceeds 3·5 atmosphere, it acts as a violent poison on all living

beings, killing plants and animals alike, and even organised ferments. The partial pressure of 3·5 atmospheres may be produced either by subjecting the gas itself to that pressure, or by compressing the air to 17 atmospheres.

Necessity for ventilation.—The necessity for free ventilation of the air in dwelling-houses follows from what has just been said. Wherever animals are crowded together, the oxygen of the air by which they are surrounded soon becomes exhausted, and CO_2 takes its place. But this is not all; the lungs and the skin alike give off other waste products, which, though minute in quantity, still make themselves perceptible in the odour of the breath and of the skin, which are characteristic of each individual, and which give the peculiarly penetrating and unpleasant odour to the dwellings of the poor, to the out-patient rooms of hospitals, and wherever the free access of air and water are neglected. Fortunately, the free interchange that takes place between gases, and the porous nature of the materials of which our garments and houses are constructed, allows a natural ventilation to take place, which requires the perverse ingenuity of man to interrupt. It may be accepted as a fact, that as soon as air becomes in the slightest degree tainted, or has a distinct odour perceptible to one who enters it from fresh air, it has become unwholesome. In ordinary air, the proportion of CO_2 is four parts in 10,000, but it has been found to rise as high as twenty or thirty parts in 10,000, whilst in some schoolrooms in Germany it has been noticed by Pettenkofer to rise as high as 72 parts in 10,000. It is generally held that to maintain the air of a room in a sufficient state of purity, 1,000 cubic feet for each individual is not too much, and no doubt, with the ordinary ventilation that is continually taking place through the chimney, and the chinks of windows and of doors, and even through

the very walls themselves, this is sufficient; but it must not be forgotten that such ventilation is absolutely necessary, and that in rooms that are unprovided with a chimney, and in which, as is sometimes done, the chinks are closed by pasting paper over them, the air soon becomes loaded with poisonous exhalations. In order that air should remain sufficiently pure for breathing purposes, at least 200 times the volume of the air expired by each individual should in any given time be added to it. In large factories, the unwholesome results of insufficient ventilation are greatly intensified by the presence of floating particles of the fabrics manufactured in them; cotton, silk, and steel filings being especially injurious. The preservation of the walls of the dwelling-houses from moisture is of great importance, for not only does moisture fill the pores of wood, brick, or other constructive material, and thus arrest ventilation in this direction, but the absorptive power of moisture for heat exercises a prejudicial influence on the inmates.

Artificial respiration.—If the entrance of air to the lungs be arrested for more than a few seconds by any means, such as smothering, choking, hanging, drowning, or if the air be impure, as in suffocation after a preliminary period of intense anxiety, and in most cases of violent spasmodic efforts to breathe, unconsciousness comes on, and the respiratory movements cease, though the heart long continues to execute feeble contractions. During this period, life, almost extinct, can be restored by practising artificial respiration, and mechanically effecting a renewal of the air in the lungs. The best mode of effecting this is to place the body on its back on a table, raising the head with a hard pillow. The wrists or the arms may then be firmly seized, raised towards the head, and then slowly brought down to the sides, strong pressure being made with them against the thorax. This proceeding

should be repeated fifteen times in the minute. Care should be taken that the tongue is brought forward and the chin raised. An audible groan or gurgling is often a sign that the air is entering well. About 20 cubic inches of air can thus be made to enter the lungs at each imitation of the normal respiratory movements. A common error is to perform the acts too rapidly and also irregularly. Recovery has been known to occur in apparently hopeless cases where artificial respiration has been persisted in for some hours.

Internal respiration.—By internal respiration is meant the exchange of gases which takes place between the tissues, including the blood itself, and the gases contained in the blood. The changes are therefore exactly opposed, so far as the gases of the blood are concerned, to the interchange of gases that takes place in pulmonary respiration. No sooner does the blood become charged with oxygen as it traverses the capillaries of the lungs, than oxydation of the more unstable compounds contained in the blood commences; not only, however, is the quantity of these substances small, but the time during which this action can take place is extremely brief, only lasting till the blood reaches the systemic capillaries; hence the oxydising processes which take place within the vessels are comparatively slight; but no sooner has the blood reached the capillaries, than it is surrounded by tissues poor in oxygen and rich in CO_2, and an active interchange of gases immediately takes place. The O of the hæmoglobin of the coloured corpuscles rapidly escapes, whilst the CO_2, with which the tissues are charged, as rapidly enters the blood. That the tension of the CO_2 in the tissues is high, is clearly shown by the tension of this gas in the fluids of the body; thus, whilst in arterial blood it is equivalent to a column of mercury 21 mm. in height, and in the venous blood

of the pulmonary capillaries to one of 41 mm., in the bile it is as much as 50 mm., and in acid urine to 68 mm., though in the latter cases it can only be derived from the tissues. In the lymph it is about 35 mm. of mercury, and the smaller tension of the CO_2 in the lymph than in venous blood may be explained in part by supposing that the processes of oxydation continue to take place in the blood, in part by the slower current of the lymph, which, perhaps, allows of a more equal distribution of the CO_2, partly to the circumstance that in the muscles, in which the production of CO_2 chiefly takes place, the lymphatics are few, and partly that the whole process of interchange is affected by chemical affinity, and that there are compounds in the blood which have a stronger affinity for CO_2 than in the lymph.

That the processes of oxydation which take place in the blood itself are small, is shown by the fact that easily oxydisable substances, such as glucose and sodium urate, may be added to blood removed from the action of the tissues, and after some time has elapsed be again recovered without having undergone oxydation; whilst that the blood in traversing the tissues rapidly loses its oxygen, can easily be demonstrated by the experiment suggested by Vierordt, in which the bright light of the sun traversing the rosy pulp of the finger is examined with a spectroscope before and after the application of a ligature to the finger near its middle. Before the ligature is applied it will be found to present the usual double absorption bands, but in the course of two or three minutes after its application these will have disappeared, and will be found to be replaced by the single band of deoxydised hæmoglobin.

Respiratory quotient.—This term has been applied by Pflüger to the relation between the volume of CO_2 exhaled by respiration and the quantity of O

consumed; this relation, $\frac{CO_2}{O_2}$, is in general less than unity, that is to say, that the whole of the oxygen consumed by the organism does not reappear in the air expired under the form of CO_2, a part being used up in forming other combinations, such, for example, as water. The study of the respiratory quotient, it is remarked by Frédéricq, has led to an interesting conclusion, viz. that the greater part of the alimentary substances, modified and transformed by digestion and afterwards absorbed into the body, only remain in it for a short period, and are then rapidly destroyed. The materials which are actually undergoing oxydation in our bodies are the combustible bodies that have but just left the alimentary canal. The proof of this is that the value of the respiratory quotient varies quickly with change of diet, and is always in relation with the food ingested. Starch, fat, albumin, in becoming oxydised in the body, require the same quantity of oxygen as if they were burnt in air. With an exclusive diet of starch, the respiratory quotient $\frac{CO_2}{O_2} = 1$, or tends to approximate unity; for hydrocarbonaceous compounds contain in themselves sufficient oxygen to convert all their hydrogen into water; they only require the additional quantity of oxygen necessary to convert their C into CO_2. So when starch is burnt in the air, the volume of oxygen consumed is exactly equal to the volume of CO_2 produced, and the quotient of combustion, $\frac{CO_2}{O_2}$, as it may be called, $= 1$. The fats and albumin contain little oxygen and much hydrogen, and the quotient of combustion, or respiratory quotient, is much less than unity. A mixed diet corresponds to the respiratory quotient, 0·86, whilst on an exclusively animal diet the quotient may descend to 0·62. It has a very different value in

herbivorous and in carnivorous animals. In any animal, however, even if an herbivorous one, subjected to strict fast, and consequently living on the fat and albumin of its own tissues, the respiratory quotient approximates that of animals placed on meat diet, being 0·76. Violent muscular exertion considerably augments the cyphers of O and of CO_2 of the respiration, but especially of the CO_2, and affects to some extent the respiratory quotient; its value then approximates unity, just as if the animal had been fed on hydrocarbonaceous diet.

Respiration by the skin.—The conditions under which the blood travels in the skin are not materially different from those which are present in the lungs. In both cases there is a rich plexus of capillaries separated from the air by epithelium. In the lungs, the epithelium forms a simple layer, whilst in the skin there are many layers, so that the contact of the air with the blood is less immediate. The gaseous interchange in accordance with this difference is much less active. The quantity of CO_2 discharged by the skin as compared with the lungs is estimated to be as 1 : 38.

The amount of insensible transpiration of vapour of water is estimated to be double that given off by the lungs, or about 2 lbs. per diem, though, of course, the amount of this vapour given off will depend on the size of the body, the temperature, and the humidity of the air.

In *sighing*, a deep inspiration is taken, and is followed by an audible expiration. It appears to be a compensatory effort to make up for several previously imperfectly performed respiratory acts.

In *yawning*, air enters through the mouth, which is usually widely opened, the nares are closed, and a deep inspiration and expiration follow. It is an indication of fatigue and inadequate working of the respiratory muscles.

In *hiccup*, an inspiration is made by contraction of the diaphragm, which is suddenly arrested by closure of the lips of the glottis.

In *snoring*, air entering through the nose and mouth causes a relaxed uvula and soft palate to vibrate strongly.

In *laughing*, a succession of interrupted expirations occurs.

In *coughing*, the glottis is at first closed, but is suddenly burst open with a resonant sound, by the contraction of the expiratory muscles, the object being usually to expel masses of inspissated mucus from the trachea and larynx.

Coughing is a reflex act, the nervous mechanism of which is that a stimulus in the form of some mechanical or chemical irritant is applied to the highly sensitive branches of the superior laryngeal nerve distributed to the mucous membrane of the larynx. The nerve waves produced by the impression travel up the superior laryngeal and vagal nerves to a co-ordinating centre situated in the medulla oblongata. From this motor impulses emanate, which, descending through the vagus and spinal cord, first excite those muscles to contract which close the glottis, and then induce powerful contractions of the muscles of expiration. The effect is that air is expelled from the lungs with great force, driving the foreign body, if there be one, from its position. In many instances irregular muscular contractions are excited and strong efforts of inspiration are made whilst the glottis is closed, giving rise to a crowing sound.

In *sneezing*, an expiration of almost convulsive violence succeeds a long inspiration, the blast of air being directed, in some instances, chiefly through the nose, and in others chiefly through the mouth.

CHAPTER VI.

FOOD.

Food.—Food is required by all animals to supply the waste of the body, and in the higher animals to maintain the temperature. Now the body of an adult consists of 58·5 per cent. of water, and 41·5 per cent. of solids, and the analysis of the body of a healthy man, and of a healthy woman, has been found to give the following results :—

Weight of Body in Grammes.

Man.	Woman.
69,688	55,400

Percentage of the Total Weight of the Body.

	Man.	Woman.
Bones	15·9	15·1
Muscles	41·8	35·8
Thoracic viscera	1·7	2·4
Abdominal viscera	7·2	8·2
Fat	18·2	28·2
Skin	6·9	5·7
Brain	1·9	2·1

Each and all of these parts undergo continual waste; some more, some less rapidly, but all of them to so great an extent that if food be completely withheld remarkable changes in volume and weight are manifest in the course of a few days. This loss is supplied by food, and as a rule the quantity daily ingested corresponds with that which is lost by the skin, lungs, urine, and fæces in the same space of time. The nature of the food is diverse, and it is

not consumed in a form that at first sight resembles the tissues it is about to nourish; it is the purpose of the digestive system to induce such alteration in it as may fit it to become a part of the body, or, in other words, to prepare it for assimilation.

If it be asked, what are the tissues themselves composed of? the reply must be, that though presenting considerable chemical and physical differences, they all spring from and contain an organic basis, protoplasm, which is composed of C, H, N, and O, with small quantities of P and S, and the chemical characters of which show that it belongs to the group of albumins. These characters are indeed often obscured by the changes it has undergone in the process of development, and the materials it has deposited in its own substance; but in some instances, as in muscle and nerve and gland, protoplasm still exists as such, and is the active agent in the functional activity of these tissues. In other instances, as in bone, calcareous salts have been deposited, which more than double its bulk, whilst in the enamel of the teeth the salts are so abundant as almost entirely to conceal the protoplasm originally present. In all instances the tissues are built up of small masses of protoplasm, named cells, each of which has its own definite destiny and purpose; some becoming converted into blood corpuscles, some into the walls of blood-vessels, and others into the structure of the different organs. In many instances, as in the cells which form the epidermis and the epithelium of mucous membrane, and the cells of the glands and of the brain, the original cell-form is preserved to so great an extent that there is no difficulty in recognising them as cells; whilst in others they are so modified by growth that it is necessary to follow them through the whole course of their development to furnish satisfactory proof that

the structure or tissue under examination is in reality formed of them. It is to minister to the wants of these variously modified cells in the discharge of their several functions that food is required.

Hunger and thirst.—Hunger is the sensation, usually referred to the stomach, of an insufficient supply of food in the economy. Thirst is the sensation, referred to the fauces, of a want of fluid in the body. Both sensations are much more acutely as well as differently felt by some persons than by others: hunger, for example, expresses itself in some people by faintness. It may be temporarily allayed by ingesting into the stomach any substance even of an indigestible nature. It can be endured for a very long period by some of the carnivora; dogs, deprived of food, live from four to nine weeks, according to their previous condition. Birds die after deprivation of food in a few days. Some mollusca, as the snail, can live, if perfectly quiescent, for a year or two without food, and even mammals, when hybernating, can live without food for some months, which is due to the circumstance that in hybernation, whilst loss of heat is prevented by the retreat of the animal to caves, burrows, and nests, the whole vital activity is reduced to its lowest ebb, and in most cases considerable surplus material has been stored up in the adipose and hepatic tissues. That the sensation of hunger is not due exclusively to the impressions made upon the gastric mucous membrane, but rather to the state of the system at large, is shown by the fact that it is not abolished by section of the vagi. Thirst is not alleviated by the section of the pharyngeal nerves, nor by the mere contact of water with the fauces. Water must first be absorbed, and the blood and tissues replenished with this fluid before the sensation is removed. Dogs in which an œsophageal fistula has been made, and which have been long deprived of

water, drink long and continuously without avail, when supplied with it, because it escapes as soon as swallowed, whereas thirst is readily quenched by injecting water into the rectum, or into the veins.

Classification of food.—The food of man varies in different regions of the earth in a remarkable manner; partly in accordance with the productions of the earth, air, or sea by which he is surrounded; but partly also in accordance with the requirements of his body as determined by the external temperature to which he is exposed, his age, and the particular form of mental, muscular, or other kind of work he performs. The Arab can support life on legumes or millet, and a few dates; the Indian on some rice and ghee, with dhurra, or on the fruit of the banana; whilst the well-fed European requires a great variety, as well as abundance of food; and the natives of the Arctic regions are compulsorily restricted to animal diet rich in oil. But it is found that however different in appearance these several dietaries may be, they contain certain proximate principles which are to a greater or less extent present in all. These are:

1. Proteids, such as the animal albumins and vegetable glutins, which form the greater part of the solids of meat, fish, eggs, milk, and bread-stuffs.

2. Farinaceous and saccharine compounds, such as starch, gum, sugar, and glycogen and inosite, the first three of which are chiefly formed by plants and the last two by animals.

3. Oleaginous compounds, such as the animal and vegetable fats and oils.

4. Inorganic compounds, such as salts and water.

It may be laid down as a rule, without exception, that none of these substances, neither albumin, nor sugar, nor starch, nor gum, nor oil, is capable of supporting life if taken alone. Whenever an animal is fed on pure albumin, oil, or sugar, it dies. There

must be a due admixture of the several proximate principles, though extraordinary variations in the relative quantities occur. In those forms of food which experience has shown to be capable of nourishing every tissue and organ of the body, the types of which are seen in the *egg*, and in *milk*, there is an admixture, though in very different proportions, of all the above-mentioned groups of proximate principles.

It was formerly considered that foods were divisible into respiratory and flesh-forming. The former were held to be merely taken to maintain, by their combustion, the heat of the body, and were hence also termed heat-producers; this class consisted of sugars, starches, and oils. The latter were considered to minister to the nutrition of the tissues, and to be essentially applied to the formation of muscle and nerve; starches and oils contain no nitrogen, and it was hence thought they could not be applied to the formation of tissue. The general result of modern research is to throw doubt upon this classification of food. We shall see that even in muscle there are non-azotised constituents which are essential components of its tissue, and without which it would not be muscle, and it therefore seems probable that even the non-azotised substances may be applied to the nutrition of muscle, though their chief office is probably to supply the force developed during its contraction; on the other hand, it is certain that proteids contain the nitrogen which the muscles and nerves require, and that they are applied to their nutrition; but there is good reason to believe that they also minister to the production of heat, and, in fact, break up into two nearly equal portions, an azotised and an unazotised portion; the former being applied to the nutrition of the azotised tissue, whilst the latter, like the starches and sugars, is applied to the development of force and to the generation of heat.

We may proceed to consider briefly the composition of some of the principal articles of ordinary diet.

Meat.—The flesh of animals as consumed at table is composed of about seventy-eight parts of water and twenty-two parts of solids, and the solids consist (1) of myosin-albumin, which is the chief constituent of the contractile muscle substance; (2) serum-albumin, derived from the lymph and blood coursing through the tissue; (3) gelatin, derived from the connective tissue; (4) elastin, from the elastic tissue; (5) special colouring material; (6) keratin, from the endothelium of the vessels; (7) products of disintegration of proteids, as kreatin, kreatinin, inosinic, and sarcolactic acids, taurin, sarkin, xanthin, and uric acid; (8) fats, with lecithin and cholesterin; (9) carbohydrates, as inosite, dextrin, grape-sugar, and glycogen: and lastly salts, amongst which the salts of potassium and those of phosphoric acid, with magnesium and calcium, predominate. In 100 parts of the salts, potassium exists in the proportion of 39·4, sodium 4·86, magnesium 3·88, and phosphoric acid 46·74. The remainder is made up of chlorine, calcium, and iron oxide.

The quantity of fat varies with the state of fattening of the animal. In man, after the visible fat has been dissected off, there still remains in 100 parts of flesh from seven to fifteen parts of fat; in beef, from eleven to twenty-two parts; in mutton, about four parts; in fowls, about three parts. The object of cooking meat is to render it more digestible. In roasting and in boiling meat, the outside should be quickly exposed to a high temperature, in order to coagulate the albumin of the surface and prevent the juices escaping from within. The joint may then be more slowly cooked. Broths should, on the other hand, be made by soaking the meat for some time in cold water, and then slowly warming. There is but

little nutriment in broth, as after careful preparation only three parts per cent. are dissolved, and about three parts remain suspended in the form of coagulated albumin. The dissolved constituents are the potash salts, kreatin and kreatinin; the salts of lactic and inosinic acids, and some extractives; lastly, gelatin. A teaspoonful of Liebig's extract represents a pound of meat, but it must not be supposed that it is in any way equivalent to that amount of beefsteak for a healthy person. It is concentrated beef-tea, and nothing more.

Eggs.—The egg is clearly a perfect form of food, since, with the exception of oxygen, it contains in itself all that is required to form the complete bird or reptile. The ovum of man, however, is extremely small, and, though containing a sufficient store of nutriment for the earliest stages of development, it soon throws out from its surface processes which, dipping into the large blood-vessels of the uterus, draw from thence the material required for further growth. The egg of the fowl is composed of the yolk or vitellus, and the white or albuminous substance, which is again enclosed in the shell. The average weight of a hen's egg is about 1·75 oz., of which the shell forms one-tenth, the white about six-tenths, and the yolk three-tenths. White of egg contains about 86 per cent. of water and 14 per cent. of solids, of which albumin forms 13 parts, globulin, 0·134, salts 0·6, with traces of fat, glycose, and colouring matter. The yolk contains about 48 per cent. of water, and 52 per cent. of solids, of which vitellin forms 14 parts, nuclein, 1·5; fats and lecithin, 30; cholesterin, 1·75; and there are some colouring matter and glycose, and about ·1 part of salts.

Vitellin is a globulin-proteid, the solution of which is not precipitated by common salt, in which respect it differs from myosin. It is easily soluble in

water containing 1 per cent. of hydrochloric acid, and is then converted into syntonin. It dissolves easily in weak solution of soda. It is precipitated by alcohol.

It is estimated that 1 lb. of hard-boiled eggs, if completely oxydised, can set free a force equal to raising 1,415 tons 1 foot high. Eighteen eggs contain an amount of flesh-forming substance and other pabulum sufficient to maintain the life of an adult man for one day.

Vegetable foods.—The most important of the foods derived from the vegetable kingdom are supplied by the cereals, and by leguminous plants, which contain both proteids and starch, and by the potato and other plants having in their fruit or seed, in root, in tuber, in leaves, or in pith, a large store of starch. Thus 100 parts of dry wheat-flour contain 16·5 parts of proteids, and 56·25 of starch. Barley contains a little more of the proteids and much less starch (13·38). Rye, less proteids and more starch. Rice has only 7 or 8 parts of proteids, but 78 parts of starch. Other constituents of the flour of the cereals are cellulose and dextrin and salts. In making bread the flour is mixed with water; salt and yeast are added, and the whole kept at a moderately warm temperature. The proteids soon begin to decompose under the influence of the ferment, and themselves act as a ferment to the starch, which becomes converted into dextrin and partially into sugar, and this decomposing yields CO_2 and alcohol; the evolution of the CO_2 gas renders bread vesicular, and the alcohol is driven off in the baking. A method is now commonly adopted by which the bread is rendered vesicular without fermenting it. This is accomplished by making the dough with water charged with CO_2 under pressure; on removing the pressure the bubbles of CO_2 enlarge and the dough swells up. In another

method the bread is kneaded with sodium carbonate, and then mingled with hydrochloric acid under pressure. On removing the pressure the gas escapes, rendering the bread light, and the sodium chloride remains.

Peas and beans contain about 28 per cent. of vegetable casein, or legumin, 38 per cent. of starch, with lecithin and cholesterin, and from 9 to 19 per cent. of water. As they contain no gluten they cannot be made into dough. The large quantity of proteids they contain, and their cheapness, render them important articles of diet in an economical point of view.

Potatoes contain from 70 to 81 per cent. of water, 16 to 23 per cent. of starch, and a small quantity, 2·5 per cent., of albumin. In 100 parts of the ash there are about 47 parts of potash, 8 parts of potassium chloride, 2·5 parts of sodium chloride, 13 parts of magnesia, 3·3 parts of lime, and 12 parts of phosphoric acid. Potatoes contain little or no sulphuric acid.

Fruits contain sugar, salts, organic acids, and a gelatinising substance named pectin $C_{32}H_{48}O_{32}$.

Green food is rich in salts resembling those of the blood, but starch, cellulose, dextrin, sugar, and albumin are all present, though only in small quantity.

Condiments.—Condiments are used partly and chiefly to stimulate the appetite, and to cover or conceal disagreeable flavours, and partly as correctives to promote digestion, stimulate the secretions of the intestinal tract, and prevent the injurious effects of certain kinds of food. Salt, mustard, ginger, cinnamon, cardamoms, cloves, capers, garlic, and oil, are amongst those commonly used for the former purpose; black and cayenne pepper, vinegar, lemon, and orange juice, amongst the latter.

Drinks.—Water is the most necessary and the most wholesome of drinks. It forms a large proportion,

58·5 per cent., of the body weight, and if the chief organs be taken separately it is found to constitute 30 per cent. of adipose tissue, 69 per cent. of the liver, 72 per cent. of the skin, 75 per cent. of the brain, 75·7 per cent. of the muscles, and 83 per cent. of the blood. It is constantly being discharged from the body by the lungs and skin, and by the kidneys and fæces. It is essential to the processes of digestion, absorption, circulation, and secretion, and is the best solvent of the products of the disintegration of the tissues. Rain water is pure, containing no salts. Spring water is charged with various salts, especially with those of calcium, sodium, magnesium, and iron. It contains usually but little oxygen, whilst it is rich in CO_2. River water, like the foregoing, is potable, but is apt to become contaminated in populous districts with excrementitious products and the refuse of factories. It requires in such cases to be purified, which may generally be accomplished by boiling it.

Drinking water should be tasteless, colourless, and destitute of smell. The lime salts should not exceed 20 parts in 100,000 parts, and these are precipitated on boiling, which reduces its "hardness." The presence of organic matter may be ascertained (1) by evaporating a large quantity to dryness and heating the residue, when a well-marked discoloration will be perceived, accompanied with the smell of ammonia; (2) by the addition of chloride of gold and potassium, which gives a blackish precipitate; (3) by the addition of potassium permanganate, which become deoxdyised and decolorised by organic matter. The presence of more than $1\frac{1}{2}$ gr. of common salt in a gallon of water indicates, though it does not absolutely prove, sewage contamination. This quantity scarcely gives more than a mere cloudiness with nitrate of silver in water acidulated with nitric acid, and a specimen of water may be tested by filling a tumbler

with it, adding twenty drops of nitric acid and five of a solution of silver nitrate. If there is more than a cloudiness common salt is in excess, and this is probably derived from urine. Drinking impure water is apt to produce typhoid fever, and to favour the spread of cholera, dysentery, and other pestilent diseases. From one to three pints per diem is sufficient for the wants of the œconomy.

Beer is obtained from an infusion of malt, which has undergone fermentation, and to which hops, or some other bitter, has been added. The sp. gr. of English beer is from 1010 to 1014. The percentage of dextrin, cellulose, and sugar derived from the malt, is from 4 to 15 per cent. The hop extract is in much smaller quantity. The alcohol varies from 1 to 10 per cent. in volume. There are some free acids, chiefly lactic, acetic, gallic, and malic. Free CO_2, amounting to nearly two cubic inches per ounce, is usually present. Excess in its consumption leads to gouty and bilious disorders due to the impaired elimination of the products of degeneration.

Wines contain from 6 to 26 per cent. of alcohol by volume; champagnes contain from 6 to 13 per cent., the Rhine wines generally about 10 per cent., port and sherry from 16 to 25 per cent. Many wines are fortified by the addition of brandy for the English market. Besides alcohol, wine contains ethers which are mainly instrumental in conferring aroma and flavour, albuminous and colouring matters, sugar, free acids, and salts. The total solids vary from 3 to 14 per cent.

Spirits.—The most common of these are gin, rum, brandy, and whiskey, which should contain from 50 to 60 per cent. by volume of pure alcohol, but which, when sold by retail, are often much diluted.

Alcohol in one form or other is used by most of

the civilised nations of the world as a stimulant. In small quantities and in a diluted condition it probably does little or no harm, but taken in excess it causes exhaustion, and leads to poverty, and vice, and misery. It is believed that under ordinary conditions of exercise and respiratory activity about $1\frac{1}{2}$ ounces of pure alcohol can be consumed or burnt off in the œconomy per diem, though in fresh air and with great muscular exertion a much larger quantity may be consumed without harm. When an excess is ingested it is only partially oxydised in the body, and the products are partly retained in the system, becoming a fertile source of disease, and are partly eliminated by the lungs and skin, communicating a peculiarly unpleasant odour to the breath. Alcohol in any form is a luxury, and is not necessary, even if it be not injurious, whenever severe mental or bodily exertion is required to be made. Its place may be advantageously supplied by tea or coffee.

Tea.—Tea-leaves contain 1·8 per cent. of thein, 2·6 of albumin, 9·7 of dextrin, 22 of cellulose, 15 of tannin, 20 of extractives, 5·4 ash. The thein is combined with tannic acid. The drink named "tea" is obtained by pouring boiling water, free, if possible, from lime and iron, upon tea-leaves, which yield six-sevenths of the soluble matters to the first infusion. Tea is stimulant and restorative.

Coffee.—Coffee berries contain 1·7 per cent. of caffein, 34 per cent. of cellulose, 10 to 13 of fat. Sugar, dextrin, and a vegetable acid 15·5, legumin 10 per cent., with an aromatic oil and salts. Coffee infusion contains most of the thein. Coffee is a stimulant to the nervous system, and in excess augments the reflex activity of the spinal cord.

Milk.—Milk is the secretion of the mammary glands, the activity of which commences at the period of delivery, continues for a period of about nine

months, and, if encouraged, may persist for a much longer period. The fluid secreted is intended for the nourishment of the infant, and contains all the materials requisite for its nutriment, growth, and development. The quantity discharged per diem varies from 500 to 1,500 cubic centimetres. Its secretion is ordinarily a reflex act, the nervous circle being *sensory branches* of the intercostal nerves, a *nerve centre* in the spinal cord, and *motor fibres* emanating from this centre to the gland; in addition, the sympathetic supplies vaso-motor fibres. It is certain that the mind exerts considerable influence upon the secretion, both in regard to quantity and quality. The sight or the cry of the infant causes a flow of blood (termed the "draught") to the breast; and violent emotions may render it unwholesome.

The sp. gr. of milk varies, but is normally about 1030. It contains about 90 parts per cent. of water and 10 parts of solids, of which proteids, fat, and sugar each constitute about 3 parts, and the salts $\frac{1}{5}$ part. On standing, the fat gradually rises, as cream, to the top; and, if churned, the albuminous envelopes of the fat globules break down, and the oil-drops, running together, form butter. The *fats* of the milk globules are the triglycerides of stearic, palmitic, myristic, oleic, butyric, and other fatty acids. The *proteids* are completely precipitated by tannin. They consist chiefly of casein, with a small proportion of serum- or acid-albumin. Casein is a form of albumin which is not precipitated at 100° C., but is thrown down in flocculi on the addition of dilute acetic or hydrochloric acid. It is also precipitated by the casein-ferment of the stomach, one gramme of this ferment being capable of coagulating 30 litres of milk. When thus coagulated, separated from the whey, and pressed, it forms cheese. The plasma of milk contains, besides

proteids, traces of urea, kreatin, lactic acid, and milk sugar.

Demonstration of the constituents of milk.—Add a few drops of acetic acid to some cow's milk in a beaker, and warm the mixture gently over a spirit lamp. A flocculent coagulum soon begins to form, which may be separated from the fluid by filtration. On washing the coagulum with ether the butter is dissolved, and the casein is left. The butter is obtained by evaporating the ether. The filtered liquid, from which the coagulum has been separated, should be boiled to precipitate albumin, filtered to separate it, and the clear fluid may then be treated with Fehling's solution, 20 cc. of which corresponds to 0·134 gramme of sugar of milk. A separate analysis must be made for the salts.

Milk sugar, which may be obtained by evaporating filtered whey, forms a crystalline mass having the composition $C_6H_{12}O_6$.

The chief *salts* of milk are sodium and potassium chloride, calcium and magnesium phosphate. The potassium salts are more abundant than the sodium salts.

Colostrum is the first milk secreted after delivery. It contains little casein, but much serum, albumin, and fat. It also contains some of the secreting cells, It has a slight purgative action.

Selection of food.—The principles by which we should be guided in the selection of food are that it should be digestible and wholesome, varied, moderately abundant, and œconomical. The power which the gastric juice possesses of arresting putrefactive processes enables "high" game and decomposing cheese, and other substances that, but for this power, would be highly deleterious, to be taken as food; but it is doubtful whether, if taken in excess, they would not prove harmful, and there is much evidence to

prove that the constant consumption of decomposing fish in hot climates is associated with, if not productive of, leprosy.

Food should be *varied*, since the persistent use of any particular kind breeds disgust, which is only overcome by absolute hunger, and would probably in no case, though it might enable life to be sustained, supply the necessary materials for the best mental or bodily work.

When food can be obtained, and is consumed by an animal in larger quantity than is required to supply the wants of the œconomy, a portion of it is stored up in various organs and tissues. The deposits of fat, and the accumulation of glycogen in the liver, are well-marked examples of this *luxus consumption*, as it is sometimes called, and the portion so stored up is again utilised in the generation of heat and nervo-muscular activity when food is scarce, or when unusual and sustained efforts have to be made.

In regard to *quantity*, it would seem to be the practice in all nations where food can be readily obtained that much more material is consumed than is absolutely required on theoretical grounds.

In regard to *œconomy* much may be said. Moleschott found that a strong and active adult soldier required per diem :

Albumin	130	grammes.
Fat	84	,,
Starch, sugar, etc. . .	404	,,
Salts	30	,,
Water	2,800	,,
Total . . .	3,448	,,
The total nitrogen is here . .	20·2	grammes.
,, carbon ,, . .	320	,,

The proportion of N to C is therefore as 1 : 15. That diet will accordingly be most œconomical in

which this proportion is observed, providing only that it is equally digestible. Moleschott has placed side by side the relative quantities of the chief substances which will afford to the consumer the 130 grammes of albumin he requires, as follows:

Cheese	388	grammes.
Lentils	491	„
Peas	582	„
Beef	614	„
Eggs	968	„
Wheaten bread	1,444	„
Rice	2,562	„
Rye-bread	2,875	„
Potatoes	10,000	„

It is obvious from this, that, if cheese be compared with potatoes, a much smaller quantity (twenty times less) is required to supply him with the necessary 130 grammes of albumin with cheese than with potatoes, and that consequently he must in the latter case consume an immense amount of superfluous nourishment.

In like manner, to obtain the 404 grammes of carbohydrates he requires, he must consume

Rice	572	grammes.
Wheat-bread	625	„
Lentils	806	„
Peas	819	„
Eggs	902	„
Rye-bread	930	„
Cheese	2,011	„
Potatoes	2,039	„
Meat	2,261	„

That is, he need only take a moderate amount of rice, but must take a very large quantity of meat, to obtain it. Hence, as common experience shows, the most œconomical diet is when he consumes bread with meat or cheese, or takes some highly albuminous compound with potatoes or rice.

Value of food.—J. Koenig estimates the money value of 100 grammes of albumin obtained from the animal kingdom to be 65 pence, obtained from the vegetable kingdom 15 pence, the proportion of the former to the latter being as 4·3 : 1. 100 grammes of fat obtained from the animal kingdom costs 20 pence, from the vegetable, 4·5 pence, or as 4·4 : 1, whilst 100 grammes of carbohydrates obtained from the vegetable kingdom costs 2·5 pence.

Diet and dietaries.—The diet of different classes in the community varies with the amount and kind of work they have to perform ; and it is often a matter of importance, not only to determine what is sufficient, but also what is least expensive. The general statement may be made that the healthy adult man performing ordinary work requires more proteids and more carbon than one who is at rest. If, as in poor-houses and in prisons, men do little work, they require less proteids, though the carbon cannot be materially reduced ; for, as we have seen, about eight or nine ounces are given off by the lungs, in the form of carbonic acid, by the healthy adult, and this is chiefly derived from the carbohydrates and hydrocarbons, or farinaceous and oily substances he consumes. Boys about ten years of age and women require about three-fourths the quantity of carbon and about one-half the quantity of flesh-formers consumed by healthy men. The following may be regarded as average dietaries for different ages :

(1) *In infancy.*—The infant should, if possible, be fed with the milk secreted by the mother. It requires from two to three pints in the twenty-four hours, which should be given at intervals of three hours. If fed at night at about ten o'clock, and be then kept warm, it will often sleep through the night. Where the mother is unable to feed the infant, the milk of the cow, ass, ewe, or goat may be substituted.

If cow's or ewe's milk be used, since both are richer than human milk, *i.e.* contain more casein and butter, but are less sweet, one-third water and a little sugar may be added to each. If artificial feeding be adopted, great care should be taken that the milk is fresh, the vessels sweet and clean, and the temperature at which it is given uniform and about 100° F. When milk cannot be obtained, good beef-tea may be given, and the fat should not all be removed. After from six to ten months feeding at the breast, the child requires some additional food, which may be bread, or arrow-root and milk, or puddings made with milk, eggs, flour, arrowroot, sago, tapioca, semolina, or cornflour. The intervals between the meals should be about three hours. In the course of the second year, brose or porridge may be given at breakfast, and a little finely cut-up fresh meat and bread, with gravy, may be given at dinner.

T. Foster found that the daily food of a well-nourished child, aged 18 months, contained albumin, 36 ; fat, 27 ; carbohydrates, 151.

(2) *In youth.*—Breakfast should consist of milk or tea or coffee, with bread and eggs, or bacon, or fresh fish, and, if liked, porridge. Dinner should not be postponed to a later hour than 1.30, and should consist of plain boiled and roast meat (occasionally exchanged for fish), potatoes, or other thoroughly-cooked vegetable, and some farinaceous pudding, with water for drink. The evening meal may consist of bread-and-butter and tea. Children under ten should be in bed by 9 p.m.

Hildesheim estimated that children from 6 to 10 years of age consumed albumin, 69 ; fat, 21 ; carbohydrates, 210. C. Voit found in one of the public institutions at Munich, children from 10 to 15 consumed daily 79 albumin, 35 fat, and 251 carbohydrates. A child 10 or 11 years of age weighs about 23 kilograms.

The following represents a sufficient diet for a healthy man performing a moderate amount of work:

Breakfast.—Three-quarters of a pint of milk; quarter of a pint of water, with coffee or tea; bread, four ounces to six ounces; butter, three-quarters of an ounce; sugar, three-quarters of an ounce; bacon, three ounces; or eggs, four ounces; or cooked meat, three ounces.

Dinner.—Cooked meat, four ounces to six ounces; potatoes, eight ounces; bread, three ounces to four ounces; pudding, eight ounces; cheese, half an ounce; soup, six ounces; water or beer, half a pint.

Tea.—Water with tea, three-quarters of a pint; sugar, three-quarters of an ounce; milk or cream, two ounces; bread, three ounces; butter, half an ounce to three-quarters of an ounce.

Supper.—Milk, three-quarters of a pint; oatmeal, one ounce; and bread, three ounces to four ounces; or eggs, four ounces; or cooked meat, three ounces; and bread, three ounces; butter or cheese, half an ounce; water or beer, half a pint.

The consumption of albumin for an adult amounts in the 24 hours to about 2 grammes of albumin for each kilogram of body weight, and for the growing child to 3·4, or 70 per cent. more.

When training for athletics, the object is to diminish superfluous fat and water, and to effect the full nutrition of the nervo-muscular apparatus; and these results are accomplished partly by judicious feeding, partly by exercise. King when in training ate for breakfast two chops, with dry toast or stale bread, and one cup of tea, without butter or sugar (the two last were probably unnecessary restrictions); for dinner, one pound to one pound and a quarter of fresh beef or mutton, toast or stale bread, a little potato or greens, and half a pint of dry old ale; for tea, one cup of tea, an egg, and dry toast; and for supper, gruel or half a pint of old ale. The exercise consisted in gentle and fast walking to the extent of at least twenty miles per day, and special exercise

in rowing or boxing, to develop certain sets of muscle.

In old age less food is required than in adult life; the work done is less, and the nutrition of the tissues is much less active. The diet should be plain, and the staple must be milk and eggs, meat, and bread, whilst wine may in most instances be taken with advantage to the extent of from four to eight ounces daily.

Diet in sickness.—The due selection of appropriate food in sickness is often a most important as well as a most difficult part of the duty of the physician. Those who are accustomed to abundant and varied food are often made to understand with difficulty that change of conditions requires a change in diet; that a man who is confined to the sick-bed, and whose muscular and mental efforts are reduced to a minimum, in whom all the vital processes, digestion, circulation, and respiration, are carried on with much less energy than usual, and who loses comparatively little heat, requires a relatively small supply of food, and that this supply should consist of thoroughly wholesome, easily digestible, and nutritious material. If food of the opposite nature be taken, it escapes digestion in the stomach, or long remains in it undigested, and becomes a source of irritation as it travels along the long tract of the intestines. At the same time it must be remembered that the internal work of the œconomy, though reduced in amount, is still performed. Even in absolute fasting, 150 grains or more of urea, representing nearly half that weight in nitrogen, is still discharged from the body by the urine, whilst a correspondingly reduced amount of carbonic dioxide and water are eliminated by the lungs. Even in absolute fasting the heat of the body must be maintained at or near 38° C. These losses must be made good. Hence, care must be taken that the food

contains a due supply both of nitrogen and carbon. Milk and its preparations, though not suitable for all persons, nor under all conditions, is yet, as a rule, the best that can be given, since it is appropriate for the digestive powers of the tenderest infant, and unites in itself all the conditions of a perfect food. Eggs in like manner, beaten up with hot coffee and with milk, supply the necessary materials for nutrition. So, too, the farinaceous foods, arrowroot, sago, rice, potatoes, semolina, or revalenta, and the like, when made with milk, are eminently digestible and wholesome; common experience has dictated the addition of milk, since they are almost completely deficient in nitrogen and in salts. Beef-tea or mutton broth, flavoured with onions or other vegetables, is useful; but it must be borne in mind that it contains very little nutritive material, and the same may be said of Liebig's, Brand's, and the other essences of food. An ox may be boiled, in a sufficiency of water to cover it, to rags, and the water may be evaporated till it occupies no greater bulk than is represented by a few small tins, but it is obvious that the concentrated essence divided amongst a party of fifty men would satisfy their wants very imperfectly as compared with a division of the original mass of meat. Such concentrated food can only be regarded as a temporary supply containing a considerable quantity of nitrogen, but wholly inadequate to maintain life for any length of time. Where very concentrated food is required, the expressed juice of fresh meat may be used. Liebig has suggested a mixture for those whose digestion is weak, which is unexceptionable in composition. It consists of 17·5 parts of fine flour, 17·5 parts of finely ground malt, 30 drops of a mixture containing 8 parts of water and 1 part of potassium carbonate, 175 parts of milk, and 32 parts of water. The mixture is kept at 60° to 70° C. for some time, till the starch is

converted by the malt into sugar, then boiled and passed through a hair sieve. The taste is pleasantly sweet.

In sickness, as a rule, raw vegetables, lettuces, celery, and fruits, should be forbidden; they are bulky, generate gases, and are not very nutritious. The due administration of alcohol requires experience. The experience of the Temperance hospitals, in which it is very sparingly administered, shows that in a large number of diseases its use may be safely dispensed with. Its chief use is to rouse the flagging energy of the nervous system and of the heart, and to act temporarily as a substitute for food. In fevers, and some other exhausting diseases, food must be given at short intervals through the night, but, as a rule, the administration of food at night, and at unusual hours, is not required.

Balance of the œconomy.—Man requires, as a rule, a diet in which the nitrogenous is to the non-nitrogenous substances as 1 : 4. It may be remembered further that the nutritive value of fat as compared with the carbohydrates (starch and sugar) is as 10 : 17.

Vierordt, who was of light weight, has given a table in which the proportions derived from experiments on himself are slightly different from that stated above, but which shows well the balance of the œconomy, or the relation of the income of the body to the expenditure. It is as follows :—

An Adult with Moderate Work Consumes

	C.	H.	N.	O.
120 grammes of albumin containing	64·18	8·60	18·88	28·34
90 „ fat „	70·20	10·26	—	9·54
330 „ starch „	146·82	20·33	—	162·85
	281·20	39·19	18·88	200·73

To this must be added 744·11 grammes of O absorbed

from the air in respiration; 2818 grammes of water consumed as drink, and 32 grammes of inorganic compounds (salts); the whole weighing about 3½ kilos, or about one-twentieth part of body weight.

An Adult with Moderate Work gives off

	Water.	C.	H.	N.	O.
	Grammes.				
By respiration ...	330	248·8	—	—	651·15
By transpiration ...	660	2·6	—	—	7·2
By urine	1,700	9·8	3·3	15·8	11·1
By fæces	128	20·0	3·0	3·0	12·0
	2,818	281·2	6·3	18·8	681·45

To this must be added 296 grammes of water, which is formed by the union of oxygen with hydrogen of the food in the body. This would contain 32·89 grammes of H, and 263·41 of O. Twenty-six grammes of salts are also eliminated with the urine, and six in the fæces.

The balance of the œconomy requires further to be considered under the heads: (1) Of inanition; (2) of insufficient supply; (3) of excessive supply.

(1) *In inanition*, although no food is taken, the animal continues to take oxygen into the system by the lungs, and to expire carbonic acid gas by the same channel, and by the skin. It still gives off urea by the kidneys. It maintains in temperate climates a temperature much above that of the surrounding air. These phenomena indicate that processes of oxydation continue, and as no supplies are introduced from without, it is clear that the animal must live upon its own tissues, and that even though it may be naturally a vegetable feeder it is now a carnivore. As might be expected, those tissues which most readily combine with oxygen are the first to waste. The fat, for example, quickly disappears, and, *cæteris paribus*, the fatter the animal, the longer is it able to sustain complete deprivation of food. Gradually, however,

the albuminous constituents are more and more drawn upon, and the muscular tissue, the solid organs of the body, as the liver, spleen and kidneys, the skin, and nervous system, contribute their portion of nutritious matter to preserve life. With the reduction of the mass of the body all the processes of life are conducted more feebly, and the loss of weight is much slower as the term of life is approached. It is estimated that for each kilo of body weight the loss of weight in man on the second day of fasting amounts to 0·13 gramme of nitrogen, and 2·59 grammes of carbon, or upon the whole he loses about 50 grammes of albumin per diem. Death usually ensues in man at the close of the third week, when the body has lost nearly half its weight. Examination of the body shows that the fat has almost wholly disappeared; the liver and spleen have lost more than half their weight; the muscles one-third; the kidneys one-fourth. The brain and heart, however, continue to be nourished at the expense of the rest of the œconomy, the brain only losing one-tenth of its normal weight, and the heart only one-fortieth part. Access to water enables life to be considerably prolonged, probably by enabling the blood to absorb the waste products of the tissues, and by promoting their combustion. The appearances presented in cases of inanition correspond with the physiological conditions. The body becomes lean and angular; the eyes sunken; the cheeks hollow from the loss of fat; the nerves and muscles lose their powers; the mental faculties become clouded, and delirium may occur; the gait is tottering; the secretions fail; the mouth is dry; sordes collect on the lips; the urine is scanty and turbid; the stomach usually contains a little acid fluid, and the gall bladder is full owing to the accumulation of the bile, which, though slowly secreted, is no longer required for digestion; the temperature slightly falls, especially towards the close of life.

(2) Akin to inanition is an *insufficient diet;* and this may be of two kinds, one in which the quantity of appropriate food is inadequate in quantity to sustain the body, and another in which the diet is limited to a particular aliment, as fat, starch, sugar, gum, or albumin. It is clear that the first four substances cannot supply the wants of the œconomy; for they contain no nitrogen, which is an essential element in the composition of the nervous, muscular, glandular, and other tissues, and the animal body is incapable of assimilating the nitrogen of the atmosphere. The utmost, therefore, that an exclusive diet of fat or of farinaceous or saccharine substances can do, is to spare the consumption of the fat and proteids of the animal's own body, and to permit these substances to be otherwise applied, and by combining with oxygen to maintain the temperature. The want of some nitrogenous food is soon perceived, and, after a brief period, the fat or starch is refused. An exclusive diet of albumin would seem at first sight to be possible, since albumin contains nitrogen, and, there is reason to believe, is capable of breaking up in the body into nitrogenous and non-nitrogenous compounds, the former of which supply nourishment to the tissues, whilst the remainder, amounting to 50 per cent. of the weight of the albumin, may be regarded as fat, and can be applied to the maintenance of heat. But, as with starch or fat, the use of a single article of diet soon produces an unconquerable aversion to it, and the subject of the experiment, whether animal or man, turns away from it with disgust.

(3) When *food is taken in excess* of the requirements of the œconomy, the body increases in weight up to a certain point, and fat is deposited; and this tendency may be intensified by hereditary predisposition, by diminished activity of mind and body, and by

cessation of the reproductive functions. A tendency to corpulency may best be met by reducing the quantity of food, and especially of the saccharine or farinaceous and oily substances.

Origin and uses of fat.—Fat is ingested into the body as fat or oil in many kinds of food. It constitutes a large proportion of the weight of all ordinary meat. It is taken in the pure form in butter, and in the oil which is so extensively used in cooking. It forms from 2 to 18 per cent. of milk, 12 per cent. of eggs, and in small proportion it enters into the composition of bread, oatmeal, and the preparations of other cereals. It was formerly thought that the supply of fat in the food was sufficient to account for all that was deposited in the tissues, and there can be little doubt that the system can rapidly seize upon and apply ingested fat to its own use.

Thus, in one experiment recorded by Hofmann, a dog was kept without food for a month, during which time its weight had fallen from about 26·5 kilos to about 10·5 kilos; it was then fed with large quantities of bacon fat for five days. In this period 1854 grammes of fat were absorbed from the intestine, and 1353 were retained in the body. The fat passed very rapidly through the blood and entered the tissues, as was shown by the circumstance that 100 grammes of the blood of the fattened animal contained only 0·08 gramme of fat; that is, the quantity of fat in the entire mass of blood in the animal was only 0·97 gramme, whilst in the liver 66 grammes of fat had been deposited. Fat does not appear to be directly deposited in the condition in which it is ingested into the body, but in most cases to undergo a process of elaboration and some kind of chemical change, since, when fat, presenting characters that enable it to be easily distinguished, is administered with the food, it cannot be recognised as forming part

of the adipose tissue of the animal, though an increase in the quantity of fat in the body may have been the result of its ingestion. To give an example: in an experiment made by Radziejewski, a dog, previously made lean by a spare diet of meat, was supplied with rape oil, one constituent of which, erucic acid, does not occur normally in animal fat; the dog increased in weight, and fat was deposited beneath the skin, in the muscles, and in the body generally, but no eruca-fat could be discovered in the newly-deposited fat. Spermaceti has been given experimentally in the same way with the same result. Late researches have, however, shown, that although part of the fat may be derived directly from the food, yet that in many cases, especially in milch cows, in pigs, and in geese, thirty, forty, fifty, or more parts per cent. of the fat so largely formed, and either deposited or secreted by these animals, must be derived from other sources, these sources being either the carbohydrates or the proteids.

Origin of fat from the carbohydrates.—If a comparison be made between the chemical composition of fats and the starches, it will be found that whilst the C and the H are nearly in the same proportion, the oils contain a much smaller proportion of oxygen; and hence, if by any means oxygen is eliminated from the starches, it is possible to obtain a substance with the composition of fat. In the process of alcoholic fermentation, such a decomposition of a compound molecule into two molecules, one of which is rich in oxygen, the other poor, is seen. The highly oxydised compound is carbonic acid, the poorly oxydised is alcohol. A similar kind of decomposition is observed when starch is fermented with cheese and chalk; alcohol and lactic and butyric acids then appear, the latter of which belongs to the fatty series. In many plants, again, which possess oily seeds, the production

of the oil as the seed ripens is accompanied by a progressive and parallel diminution of starch. In animals of carnivorous habits, which take little non-nitrogenous food, the production of fat is insignificant; but when these animals are fed on mixed diet, they soon deposit fat in their tissues; and since the fat which each animal forms and accumulates is special and peculiar to itself, and does not pre-exist in the food, there is some *prima facie* evidence that it is derived from the decomposition and chemical changes taking place in the carbohydrates. Further evidence that fats may be produced in the animal organism from the carbohydrate is obtained from the fact that bees maintain their health and weight, and yet supply wax for their cells, when fed on pure honey or sugar, free from wax; and men employed in sugar plantations become fat during the harvest of the canes, when they consume much sugar. From a chemical point of view, however, the transformation of starch or sugar into fat is difficult to explain; it probably only takes place to a small extent in carnivora; and it has been observed, that if the proteids are entirely absent from their food, even bees cease to form wax.

Origin of fat from proteids.—Many facts tend to prove that fat may be derived from the disintegration of the proteids. In the first place, when albuminous compounds, such as casein, are treated with caustic potash, or are allowed to putrify, various members of the series of fatty acids make their appearance, such as butyric, lactic, valerianic, capronic, caprylic, and caprinic acids. Secondly, under certain not well-understood conditions the muscles and other azotised constituents of the body become converted into adipocere, which is composed of the lime and ammonia soaps of the higher fatty acids. Thirdly, a kind of fatty infiltration or degenerative process appears to take place when albuminous compounds are

introduced and retained in the peritoneal cavity of living animals. Fourthly, Burdach has shown that in some animals the dried substance of the completely developed egg contains three times more fat than that of the egg just discharged from the ovary, the proportion of albumin being at the same time considerably diminished; and this late appearance of fat seems to show that it plays a comparatively minor part in the earlier and more vigorous period of developmental activity, and that it is associated with a period of arrest of activity, or at least with slower changes in the chemical processes. Fifthly, in phosphorus poisoning there is a greatly increased disintegration of the albuminous constituents of the body, whilst the absorption of oxygen and elimination of CO_2 is diminished, yet simultaneously there is a great accumulation of fat in the body. The conclusion is therefore drawn that the proteids are decomposed into nitrogenous and non-nitrogenous substances, one of the latter being the fat that is stored up, and which, perhaps, spares the consumption of the carbohydrates. Lastly, in Pettenkofer and Voit's researches good evidence was obtained, that whilst almost all the nitrogen given to well-fed dogs in their meat reappeared in the urine, a large proportion of the carbon was retained in the body; and in bitches giving milk the largest percentage of fat in the milk was obtained when the animals were fed on meat, no increase occurring when fat was added to the food. Voit believes that the proteids are capable of furnishing 51·4 per cent. of their weight of fat.

Additional evidence of the formation of fats from the proteids may be adduced in the formation of fat at the expense of casein in Roquefort cheese; and it may be further shown that the larvæ of flies, placed on coagulated blood, which contains but little fat, contain in the course of a few days ten times more fat than before.

It is not difficult to trace the changes the fats undergo when introduced into the body till they reach the blood through the lymphatic system, but their subsequent destination or career has not been ascertained. That they are absorbed by the lacteals there can be no doubt, and Hoppe Seyler remarks that although the current in the lymphatics leading from the intestines is always greater after food than in the fasting condition, yet the current in the thoracic duct is really strong in the living dog only when fat has been consumed. He found that in what he regarded as normal chyle in the thoracic duct, the proportion of fat was 7·2 in 1,000 parts, and of soaps, 2·35; but another observer has found it to vary from 2·5 to the minimum quantity of 146 per 1,000 (Zawilski). The serum of blood withdrawn from the body after a meal containing much fat, is cloudy from fat molecules, probably from the entrance of the chyle which has traversed the lacteals, lymphatic glands, and thoracic duct; but the serum soon becomes clear again, and, as a rule, contains little or no fats or soaps. A remarkable reduction in the quantity of fat in the blood takes place during its passage through the liver, one analysis showing that the quantity of fat in the portal venous blood was 5·75 per 1,000, whilst in the hepatic venous blood of the same animal it had become reduced to 0·97 per 1,000 (Drosdoff); and it is well known that with abundant food and little exercise the liver has a tendency to store up fat; the average weight of the liver of a goose, for example, is 57 grammes, but when fed on maize and kept in confinement it rises to 500 grammes, the increase being chiefly due to the augmentation in the fat.

Physiological value of fat.—Fat fulfils many purposes in the animal œconomy. The thick layer that invests the body generally, protects the deeper lying and more important organs from the injurious effects

of blows and concussions and the less severe kinds of penetrating wounds. It also diffuses pressure as in the case of the hands and soles of the feet, and the buttocks. It forms a covering which resists loss of heat by conduction; a special exemplification of its value in this respect being offered by the thick masses of blubber which enables the whale to maintain its high temperature in the intense cold of the Arctic seas. It fills up the hollows of the muscles and gives a flowing contour to the figure. In the case of the heart it facilitates its movements by rendering its surface smooth, and in that of the eye it forms an elastic bed on which its rolling movements are performed with ease. In the case of the mamma, it not only protects the mammary gland from injury and from sudden changes of temperature, but also to a certain extent prevents the lactiferous ducts from collapsing when the infant is at the breast.

But apart from these mechanical uses, the oils and fats possess a high dietetic value. The very large relative proportion of carbon and hydrogen as compared with oxygen in each molecule renders them eminently adapted for the maintenance of the heat of the body, and in burning they yield a far larger quantity of heat than the carbohydrates. Their value in this respect is further shown by their almost total disappearance in prolonged fasting, when it is probable that they are gradually oxydised.

CHAPTER VII.

DIGESTION OF FOOD.

The first acts to which solid food is subjected when introduced into the mouth are those of mastication and insalivation.

Mastication.—Mastication is effected by the movements of the movable lower jaw against the fixed upper jaw, in both of which teeth are implanted, aided by the tongue and the secretion of the salivary glands.

The teeth are divisible into groups, each having its own function. There are in each jaw four incisors, having cutting edges for the purpose of prehension and detachment of morsels of food of appropriate size; two sharp-pointed canines or laniary teeth, for piercing hard objects and tearing the food; and four bicuspids and six molars, having broad and irregular surfaces, for grinding the food and reducing it to a pulp by mingling it with the saliva.

The jaws are ordinarily kept in apposition by the pressure of the air when the mouth is closed; for this cavity is then perfectly free from air, and the pressure exerted is equal to a column of mercury of about 3 mm. in height.

The descent of the lower jaw is effected by its own weight, aided by the platysma and by the anterior bellies of the digastrics, the mylo-hyoid and genio-hyoid muscles, which are enabled to act by the fixation of the hyoid bone and larynx, by the sterno-thyroid and thyro-hyoid, and by the sterno- and omo-hyoids. The elevation of the lower jaw is accomplished by the combined action of the temporal, masseter, and internal pterygoid muscles. The forward movement of the lower jaw is effected by the

external pterygoid, the backward movement by the internal pterygoid. Lateral movements are effected by the alternate action of the pterygoids of opposite sides. The accumulation of food between the teeth and the cheeks is prevented by the contraction of the buccinator muscle and the orbicularis oris.

The *motor* nervous supply is as follows:

1. The temporal
2. The masseter
3. The pterygoids
4. The buccinator
5. The mylo-hyoid
6. The anterior belly of the digastric

} are supplied by motor branches of the third division of the fifth nerve.

1. The genio-hyoid
2. The omo-hyoid
3. The sterno-hyoid
4. The sterno-thyroid
5. The thyro-hyoid

} are supplied by the hypoglossal nerve.

1. The posterior belly of the digastric
2. The stylo-hyoid
3. The muscles of the lips

} are supplied by the facial.

The *sensory nerves* are the fifth, ninth, and tenth cerebral nerves. The *nerve-centre* presiding over the movements of mastication is situated in the medulla oblongata.

The teeth appear in a certain succession which it is important to remember, since the order in which the teeth are cut affords one of the best means of determining the age of a child. There are two sets of teeth, a first, deciduous, or milk set, and a second, or permanent set.

The deciduous teeth are twenty in number, and appear in the following order:

Four central incisors	(lower jaw earlier than upper) .	7th month after birth.
„ lateral incisors		8—10th „ „
„ anterior molars		12th „ „
„ canines		14—20th „ „
„ posterior molars		18—36th „ „

The permanent set number thirty-two, and these teeth are cut in the following order:

First true molars	7th year.
Central incisors	8th year.
Lateral incisors	9th year.
First bicuspids	10th year.
Second bicuspids	11th year.
Canines	12—13th year.
Second molars	12—14th year.
Third molars (wisdom teeth)	18th year, or later.

Insalivation.—During the act of mastication, and principally to facilitate this act and that of deglutition, the food is incorporated with saliva, which is secreted by the salivary glands, and is abundantly discharged into the mouth, from whence it may be obtained by allowing it to fall into a vessel; but, to obtain the secretion of particular glands, a cannula must be introduced into the duct of the particular gland the secretion of which it is desired to investigate.

Mucous and serous glands.—The salivary glands present examples of the two types of glands recognised by histologists as the serous or albuminous and the mucous. The parotid is an example of the serous gland. The cells are polygonal; the contents are granular; the granules staining with carmine, and being disseminated through a clear albuminous matrix. During the intervals of secretion the granular matter diminishes, whilst the clear substance augments in quantity, and appears to be the immediate precursor of the proper secretion of the gland. During the period of activity of the gland the clear matrix disappears, whilst the granular matter augments.

The mucous glands are typified in the sublingual and submaxillary glands of the dog, and in the mucous glands of the respiratory and digestive tracts. They contain two kinds of cells, one set of large size containing a nucleus, situated near the attached extremity

of the cell, surrounded by a little granular matter. The rest of the cell is filled with clear mucilaginous matter, which does not stain with carmine, but is precipitated by acetic acid. During secretion the cells yield up their mucigen, and are probably destroyed. The other set of cells forming the lunules of Giannuzzi are granular, and are distributed here and there between the mucigenous cells and the basement membrane. They probably replace the former cells in the intervals of the activity of the gland. The salivary glands are divisible into two sets, the most important of which, including the submaxillary, sublingual, and the parotid glands, lies external to the oral cavity, whilst the other, including the labial, buccal, palatine, and lingual glands, is embedded in the walls of the mouth.

Characters of the saliva.—The secretion of the *parotid gland* is thin, has an alkaline reaction and a specific gravity of 1003 or 1004. It contains 98·5 per cent. of water and about 1·5 of solids, the most important of which is a ferment named ptyalin and salts, amongst which sulphocyanide of potassium is interesting. This salt gives a red colour with iron chloride and sets free iodine from iodic acid, which may be recognised by a blue colour appearing on the addition of starch.

Submaxillary saliva is strongly alkaline; it contains mucin precipitable by acetic acid, the ferment ptyalin, and salts, amongst which potassium sulphocyanide is again present.

Sublingual saliva is alkaline, tenacious from containing much mucin, has numerous salivary corpuscles, and a trace of potassium sulphocyanide.

Mixed saliva is alkaline, has a specific gravity of 1005—1009. It is cloudy from the presence of epithelial scales and salivary corpuscles, which perform amœboid movements, fragments of food, filaments of an alga, named leptothrix buccalis, and some

other mineral organisms. It, of course, contains ptyalin, mucin, and salts. The total quantity of saliva secreted per diem varies from 200 to 1,500 grammes.

Uses of the saliva.—In connection with the digestive act the saliva (1) moistens the food and promotes mastication and deglutition, for, as a rule, the drier the food the more saliva is secreted; (2) it dissolves saccharine, saline, and various sapid substances; and (3) it exercises a saccharifying or diastatic power on starch. This action is effected through the agency of the ptyalin or hydrolytic ferment it contains, and seems to be of a complex nature, starch paste becoming in part converted first into soluble starch or amylodextrin and erythro-dextrin, which last reddens with iodine, and then successively into achroo-dextrin, which does not give any colour with iodine, maltose, and grape sugar; whilst part resists the action of the ptyalin beyond the stage of achroo-dextrin. Stating the changes shortly and excluding the intermediate changes, the action of saliva is to cause dextrin to take up an equivalent of water, converting it into glycose. Thus,

Starch. Dextrin. Dextrin. Glycose.

$$C_6H_{10}O_5 = C_6H_{10}O_5 \qquad C_6H_{10}O_5 + H_2O = C_6H_{12}O_6.$$

Apart from its use in digestion, saliva (1) moistens the mouth and enables the functions of taste to be duly performed; (2) it facilitates the movements of the tongue in speech; (3) it contains potassium sulphocyanide, which tends to prevent the decay of fragments of food lodged between the teeth, and the development of leptothrix and other fungi; (4) being constantly secreted, it occasions frequent acts of deglutition, which open the Eustachian tube and equalise the pressure of the air within and without the tympanum.

Ptyalin.—The active ferment of the saliva, ptyalin, may be obtained by acidulating saliva with phosphoric acid and adding lime-water. The precipitate

of lime phosphate which falls, carries down with it ptyalin and proteids, and from this it may be obtained by washing the precipitate with water, and precipitation from the watery solution by means of alcohol. The temperature at which ptyalin acts best as an amylolytic agent, that is, at which it is capable of converting starch into sugar most energetically, is between 38° and 41° C. It is arrested at 60° to 70° C. It is most efficient in a neutral fluid. A definite quantity of starch paste only can be converted into glycose by a limited amount of ptyalin, and a large excess of sugar interferes with its action. Ptyalin acts much more quickly on boiled starch than on the raw material. With boiled starch the presence of sugar can be demonstrated in a minute or less after admixture with saliva, whilst with raw starch from half-an-hour or two or three hours is required. An estimate of the quantity of sugar present may be obtained by allowing the fluid to ferment and collecting the CO_2 given off. 100 parts of CO_2 by weight correspond to 204·54 of sugar.

For the tests for grape sugar *see* page 11.

The saccharifying action of ptyalin on starch takes place best in neutral or in slightly alkaline solutions. It is impeded or arrested by so small a degree of acidity as is produced by 0·02 per cent. of hydrochloric acid. Hence it is stopped when the contents of the stomach are strongly acid, though it may recommence when the acids present are neutralised. Ptyalin is only contained in the saliva of the parotid gland of the new-born child, but at a later period in that of all the glands.

Innervation of the salivary glands.—The secretion of saliva is a reflex act. The nervous mechanism implicated consists of afferent or sensory fibres, a nerve centre, efferent or secretomotor fibres, and vasomotor fibres. The spinal *nerve centre* presiding over the process is situated either at the level of the

facial nucleus or a little above it, and the psychic centre is probably near the sulcus cruciatus.

The *afferent* nerves are, (1) the *Fifth*, and (2) the *Glosso-pharyngeal*. The *secreto-motor* nerves are (1) the *chorda tympani* of the facial, and (2) the *sympathetic*, the former causing dilatation, the latter contraction of the vessels. The glands may also be excited to action through the olfactory nerve and by the gastric terminations of the vagus.

Under ordinary circumstances, in the act of mastication the afferent branches of the fifth nerve and of the glosso-pharyngeal nerve conduct gustatory impressions from the tongue or palate, according to their distribution, to the medulla oblongata, and excite the gustatory centre situated in that region to originate impulses that travel to the glands through the facial and sympathetic nerves, and stimulate them to secrete saliva. The facial and sympathetic nerves are therefore said to contain *secreto-motory fibres*. The secreto-motor fibres of the facial for the submaxillary and the sublingual glands run in the *chorda tympani*. This nerve is given off from the facial in the aqueduct of Fallopius, then, crossing the tympanum, it emerges by the canal of Huguier, and is applied for a short distance to the lingual branch of the fifth, but soon separates from it; and after entering into the formation of the submaxillary ganglion or plexus, is distributed to the submaxillary and sublingual glands. The *sympathetic fibres* proceed from the plexus surrounding the facial artery. The action of these two nerves upon the submaxillary gland of the dog, where it has been chiefly investigated, is remarkable. Both nerves contain fibres that act upon the blood-vessels of the gland. When the *chorda tympani* is stimulated the vessels enlarge, and more blood passes through them, and this nerve must either contain fibres that cause the muscular coat to dilate

actively, or fibres which inhibit the action of the sympathetic and permit their coats to dilate passively. Under any circumstances, the action of the chorda when stimulated is that of a vaso-dilator. When the *sympathetic* is stimulated the vessels contract in diameter and less blood passes through them. But stimulation of these two nerves has another effect. It causes an alteration in the quality of the secretion. When the chorda tympani is stimulated the secretion is limpid and abundant. When the sympathetic is stimulated the secretion is scanty and more viscid. Both nerves, therefore, in addition to fibres influencing the size of the vessels, contain fibres that stimulate the salivary cells to secrete. But it may be said the effects on the secretion are just those which might have been expected from the influence of the nerves on the circulation. The facial nerve, or the chorda tympani (which is the same thing, since the fibres given off by the facial nerve to the gland run in the chorda tympani), when stimulated causes dilatation of the vessels, and a more rapid circulation through the gland. Hence, the secretion is thin and copious; the sympathetic fibres contract the vessels and diminish the flow of blood through the gland, and therefore when they are stimulated the secretion is slower, and it is more tenacious and of higher specific gravity. What need, then, is there to admit the existence of secreto-motory nerves? The reply is that the activity of the circulation and the activity of the secretory process bear no direct or necessary relation to each other, for (1) on stimulating the chorda tympani secretion takes place even though the vessels supplying the gland have been ligatured; (2) if atropia be subcutaneously injected into an animal and the chorda tympani be stimulated, it will be found that the vessels dilate and a greatly augmented quantity of blood passes through

the gland, but that there is no increase in the quantity of saliva, from which it would appear that the alkaloid has had no effect upon the vaso-dilator fibres, but that it has paralysed the secreto-motor fibres ; (3) it has been ascertained by direct measurement with the manometer that the saliva is secreted under a pressure greater than that of the blood in the blood-vessels, in fact, in some instances, amounting to nearly double this pressure. From these several circumstances it is concluded that the facial nerve contains fibres which directly stimulate the gland cells to secrete, and Pflüger believes that he has actually followed nerve fibres into the gland cells. It is concluded from analogy that the sympathetic also contains two sets of fibres, a vaso-constrictor and a secreto-motor set. When all the nerves distributed to the gland are divided a thin saliva is continuously secreted, named *paralytic saliva*, which only ceases when the nerves have undergone complete degeneration.

The nervous mechanism of the parotid gland is less certainly known, but the afferent fibres are contained in the fifth, and the gland can be made to secrete by stimulation of the nervus petrosus superficialis minor, a branch of the facial which is joined in the tympanum by a branch from the glosso-pharyngeal.

The fibres then run to the otic ganglion, and join the auriculo-temporal nerve, through which they reach the gland. The gland receives sympathetic fibres from the plexus surrounding the internal maxillary artery.

Atropine and daturine check the secretion of saliva in the dog, whilst pilocarpin, eserin, and curare, stimulate it. In the cat, however, a small dose of atropine causes abundant secretion of ropy saliva. The salivary centre in the medulla oblongata can be directly excited by the electric stimulus, or by the circulation through it of venous blood as in asphyxia. That there is a psychic centre is shown by

the free flow of saliva that occurs in a hungry man at the sight or even on the thought of savoury food.

Phenomena accompanying stimulation of the secreto-motor nerves.—The gland becomes more vascular. The arteries dilate, the veins convey scarlet blood, and may, owing to the enlargement of the capillaries permitting freer passage of blood, pulsate. The temperature rises a centigrade degree or more. The secretion augments in quantity.

Movements of the tongue.—These are of importance in subjecting the food equally to the crushing action of the teeth, in separating it into morsels fit for deglutition, and in pressing each morsel backwards to the fauces, where the act of deglutition commences. The complexity of the muscular fasciculi of the tongue enables it to be moved in all directions. It is protruded by the genio-hyoglossus, styloglossus, and palatoglossus, aided by the longitudinal fasciculi; depressed by the hyoglossus; elevated towards the tip by the anterior part of the superior longitudinal fibres; towards the middle by the action of the mylo-hyoid, which elevates the hyoid bone; towards the base by the styloglossus and palatoglossus, and by the stylo-hyoid; turned to either side by the contraction of the longitudinal fasciculi of the side to which it is turned. Hollowing of the dorsum is effected by the contraction of the genio-hyoglossi, aided by the transverse and vertical fasciculi. Most of the muscles of the tongue are supplied by the hypoglossal nerve; the mylo-hyoid receives branches from the fifth; the stylo-hyoid from the facial.

Deglutition.—The food taken into the mouth having been reduced to a pulp by the acts of mastication and insalivation, which should be thoroughly performed, is divided into boluses of appropriate size by the tongue, and pressed back by it to the anterior pillars of the fauces, where deglutition,

which is an involuntary act, commences. The dorsum of the tongue is rendered prominent and arched by the styloglossi, which press the bolus backwards until it is seized by the palato-glossal and palato-pharyngeal muscles; then, secondly, the soft palate is raised and stretched by the levator and tensor palati of each side, which shut off the opening of the nares, and render the dorsum an inclined plane by which the food is guided into the grasp of the constrictors of the pharynx. The bolus in this course has to travel over the upper opening of the glottis, which is a critical moment, and the entrance of food into the trachea is very carefully guarded against. To prevent it the whole larynx rises by the action of the genio-hyoid and by the anterior belly of the digastric and mylo-hyoid muscles, whilst the epiglottis is drawn downwards, which effectually occludes the orifice, and, as an additional protection, the rima glottidis is closed. By the peristaltic action of the constrictors from above downwards the mass is finally propelled into the œsophagus, through which it is driven into the stomach.

The nerve *centre* for the acts of deglutition is situated in the medulla oblongata; the afferent fibres belong to the fifth, which supplies the velum palati; to the glosso-pharyngeus, which is distributed to the tongue and pharynx, and to the superior laryngeal branch of the vagus, which supplies the epiglottis and rima glottidis. The *motor* nerves are derived from the hypoglossus supplying the tongue; the glosso-pharyngeus supplying the muscles of the pharynx, the facial supplying the levator palati (peristaphylinus internus); the fifth supplying the tensor palati, the suprahyoid muscles and the muscles of mastication; and the vagus supplying the muscles of the larynx, and of the œsophagus.

The **gastric juice.**—The glands of the stomach secrete a fluid that possesses strong digestive powers. It may be obtained by making a gastric fistula, or by

introducing a clean sponge into the empty stomach a dog, and giving the animal some fragments of cartilage to digest for a short time, and after a few minutes withdrawing the sponge. It is a nearly clear, slightly yellowish, acid fluid, which does not cloud on boiling. Its specific gravity is 1002·5, and it contains one half part per cent. of solids. The quantity secreted varies from a few to many ounces, according to the nature and quantity of the food. It contains (1) *free hydrochloric acid* in the proportion of two parts in 1000; (2) *pepsin*, a special hydrolytic ferment, in the proportion of three parts in 1000; (3) a milk curdling ferment; (4) *salts*, of which sodium and potassium chloride are the chief, two parts in 1000; (5) *mucus*; after the use of particular articles of food, as milk and butter, lactic and butyric acids may occur.

Origin of the chief constituents of the gastric juice.—The glands of the stomach are disposed vertically to the surface of the mucous membrane, and are either simple or more or less branched. They are lined by cells, and enclosed in a lymphatic space which is closely invested by a plexus of capillaries. Two sets of glands can be distinguished; those of the cardiac extremity and body of the stomach, and those of the pyloric extremity. The glands of the cardiac end are lined by two kinds of cells, the small chief *principal* or spheroidal cells, also called *adelomorphous* cells, and the *parietal*, *ovoid*, or *delomorphous* cells. The chief cells are transparent, and finely granular; the parietal cells are granular, staining deeply with osmic acid, and with aniline blue, and do not, like the chief cells, form a continuous, but an interrupted and irregular layer. The glands of the pyloric end of the stomach present only one kind of cell lining their interior, but owing to the difficulty of obtaining perfectly fresh specimens of the human stomach, it is doubtful whether they most resemble

the "chief" or the "parietal" cells. It is believed that chlorhydric acid and pepsin are formed by different cells; and that whilst the former is the product of the parietal cells, pepsin is formed by the "chief" cells; and this opinion is founded on the fact that if the stomach be ligatured near its centre, the pyloric half yields a fluid containing pepsin, but little or no acid, whilst the cardiac half yields a fluid containing both acid and pepsin. Additional arguments may be found in the circumstance that if some glands of the cardiac extremity of the stomach be isolated and warmed, they may be observed, on the addition of a little hydrochloric acid, to dissolve with rapidity, excepting only the nucleus and a small granular residue, whilst the parietal cells under similar circumstances only become transparent and swell up, resisting solution for a considerable period. But it may reasonably be concluded that the solvent action would be most noticeable in those cells which contain most pepsine, and, hence, in all pyloric cells. The deep extremities or cul-de-sacs of the gastric glands, which are for the most part lined with "chief" cells, yield, when macerated with chlorhydric acid, a better artificial gastric juice than the more superficial portion. Lastly, the chief cells undergo periodical variations, which are in direct relation with the secretion of the gastric juice; for during fasting the chief cells are large, rich in clear substance, relatively poor in granular protoplasm. The gastric mucous membrane is, at this time, strongly charged with pepsine or pepsinogen substance, the propepsine of Schiff. After secretion has taken place for some time, the clear pepsinogen substance formed at the expense of the albuminoids is discharged from the cells into the lumen of the glands, and though it still continues to be formed, the supply gradually becomes unequal to the demand, and the clear substance diminishes in the

chief glands, which exhibit, after a few hours' digestion, a granular aspect. The "chief" cells are developed at a later period than the parietal cells. Bernard endeavoured to prove that the pepsine and chlorhydric acid were secreted separately by an ingenious experiment. He injected into the jugular vein of a dog, first, a solution of lactate of iron, and then, after an interval, a solution of potassium ferrocyanide. In an acid solution these substances react on each other and form Prussian blue. The animal was killed in the course of three-quarters of an hour, and the surface of the gastric mucous membrane was deeply stained with a blue tint, whilst the rest of the gland tissue was uncoloured. He therefore attributed to the superficial cells of the gastric membrane the *role* of secreting the acid, whilst the pepsine was formed in the deeper part of the glands. It is possible, however, that the cells might have excreted the acid, which accumulates on the surface, but is never at any moment sufficiently abundant in the parietal cells to cover the alkaline reaction of the protoplasm in their interior. The intravenous injection of pilocarpine causes an abundant secretion of gastric juice.

The origin of the acid has been attempted to be explained on chemical grounds by the fact that there are fluids of alkaline reaction which may contain two acid and mutually inoffensive salts, but still have an alkaline reaction, because the acid reaction is obscured; for instance, a solution of neutral sodium phosphate Na_2HPO_4 and acid sodium phosphate NaH_2PO_4 is alkaline. Such a solution placed in a dialyser after a short time gives up its acid salt to the surrounding distilled water, and thus there remains in the dialyser an alkaline fluid, whilst outside of it is an acid fluid. Further, if neutral phosphate of soda be mixed with calcium chloride $CaCl_2$, we get calcium

triphosphate, sodium chloride, and free hydrochloric acid, as in the following equation:

$$2Na_2HPO_4 + 3CaCl_2 = Ca_3PO_4 + 4NaCl + 2HCl.$$
(Ewald.)

But hydrochloric acid possesses a high diffusive power; it passes three times as quickly through the dialyser as common salt, and hence, once formed in the blood, it may easily pass into the gastric juice. Such chemical theories are, however, not very satisfactory, and the production of the acid, like that of the ferment, must be regarded as a special property of the protoplasm lining the cells of the gastric glands. It is certain that the elimination of a large quantity of acid by these cells leaves so much alkali in the blood that when the stomach is in full digestion the urine, usually acid, becomes neutral, or even faintly alkaline, and often cloudy from precipitation of some of its salts.

Pepsin.—The active principle of the stomach is a soluble hydrolytic ferment named pepsin. It may be obtained, in a more or less pure state, in several ways. (1) By making a glycerin extract of the gastric mucous membrane of a recently-killed pig or other mammal, and treating it with alcohol. A white precipitate falls, which is soluble in water, and acts like pepsin. (2) By extracting the mucous membrane with a 3 per 1000 solution of hydrochloric acid. (3) By rubbing down the membrane with 5 per cent. of phosphoric acid, and allowing the digestive process to take place upon it for a short time. On the addition of lime-water a voluminous precipitate falls, which carries with it the pepsin. The mass is washed with water, and treated with weak hydrochloric acid. To this fluid, containing the pepsin, a solution of cholesterin in four parts of alcohol and one of ether is added, when a second voluminous precipitate falls

which again contains the pepsin. The precipitate is washed with a weak acetic acid, and the cholesterin is finally dissolved away by ether.

Origin of pepsin.—In regard to the origin of pepsin, the experiments of Langley seem to show that this substance is formed from the granules seen in the gland cells of the stomach in the living state; for, in the first place, in the various animals he examined the cell granules diminish in number and size during digestion. Secondly, during fasting the number of granules contained in the gland cells diminishes, which is in accordance with the fact that during fasting the amount of pepsin contained by a definite weight of gastric mucous membrane diminishes; and lastly, the amount of pepsin contained by any portion of the stomach is in direct proportion to the number of granules contained by the "chief" cells of that portion in the living state. He names the substance stored up by the gland cell "zymogen," and believes that it is this material from which pepsin arises when the cell secretes.

When the stomach is empty it is quiescent, presents a pale rosy tint, and contains little or no gastric juice, but the surface is covered with a thin layer of mucus. No sooner is food introduced than, apparently by a reflex action taking place through the sympathetic centres and the fibres of Meissner's plexus, the circulation quickens, the vessels enlarge, the colour of the mucous membrane becomes deeper, the venous blood returning from it is of a brighter hue, and gastric juice is poured forth from the glands.

Action of the gastric juice on proteids.—The essential action of the gastric juice on the food entering the stomach is to seize upon the proteids, and convert them from colloidal and insoluble substances into soluble or crystalloid compounds, so that they easily enter the blood. All varieties of

albumin are converted into peptones. The action of the gastric juice on albumin may be observed outside of the body by placing small cubes of white of egg in the pure juice obtained from a gastric fistula, or in an artificial juice made by adding a 3 per 1000 watery solution of hydrochloric acid to pepsin in the proportion of 2 per 1000, and maintaining the mixture at a temperature of 37° or 38° C. (97° F.). In the course of an hour or two the edges of the cube will be found to be swollen and hyaline, and ultimately a large portion undergoes solution in the fluid, especially if the process be assisted by gentle agitation.

There seem, however, to be several successive and tolerably constant steps or stages in the process. The first action of the pepsin in combination with the acid of the gastric juice is to convert albumins into syntonin or acid albumin, which is identical with the parapeptone of Meissner. The syntonin can be precipitated by simple neutralisation of the fluid, and is soon converted into a substance variously named hemialbumose (Kühne), acid peptone (Meissner), and propeptone (Schmidt-Mulheim), which is characterised by the facility with which it dissolves in water, and which gives the usual colour of a peptone with liquor potassæ and a drop of $C_{22}SO_4$. It differs from true peptones, however, by being precipitated from its solution by potassium ferrocyanide, by nitric acid, by sodium chloride, and by magnesium sulphate. By the further action of the gastric juice, propeptone is converted into peptone. The succession of changes is, therefore, albumin, propeptone, and peptone.

Slight differences exist between the peptones of albumin, casein, glutin, and other proteids. The general characters of peptones by which they are distinguished from albumins are: (1) That they are soluble in water. (2) That they do not coagulate when heated. (3) That on the addition of an alkaline solution,

and a drop or two of solution of copper sulphate, a purplish colour, differing from the pure violet of soluble albumin, is produced. (4) When much diluted, solutions of peptones are not precipitated by nitric or acetic acids, or by neutral salts of soda and magnesia. (5) With strong nitric acid they give the xanthoproteic reaction. (6) They are not precipitated when treated with strong acetic acid and ferrocyanide of potassium. (7) They are precipitated from neutral or weakly acid solutions by solution of corrosive sublimate, nitrate of mercury, nitrate of silver, and of tannic, phosphomolybdic and phospho-tungstic acids. Lastly, when injected into the blood they do not reappear in the urine in the form of albumin. It may be demonstrated that nearly twelve times more peptone will pass through an animal septum than albumin. If the gastric juice be allowed to act for a long time on peptones, leucin, tyrosin, and other products of the disintegration of albumin appear. The conversion of albumins into peptones only takes place in the presence of an acid, and, although it may be imitated outside of the body, the action is much more rapid and perfect in the body. This is due (1) to the circumstances that, in the stomach, each portion of peptone as it is produced is at once removed by absorption, which is of course impossible in artificial digestion; and (2), which is still more important, fresh acid and fresh pepsin are continuously secreted in gastric digestion, and, it is not improbable, in proportions adapted to the matters that have to be dissolved. In the case of Alexis St. Martin, a young Canadian, who, as the result of a gunshot wound, had a fistulous opening into the stomach, Dr. Beaumont found that meat was digested and absorbed in the course of two hours, that required eight or ten hours to be completely digested when submitted to the action of artificial gastric juice. No absolute period for the digestion of food can be laid

down, since it varies with the duration of the previous fast, the amount of exercise taken, the quantity and the quality of the food ingested, and the state of the health.

Milk is immediately coagulated in the stomach, owing to the precipitation of casein; and since this takes place when the free acid is neutralised, and does not take place when pure pepsin is added to milk, it is believed that a special ferment, named by Hammarsten *lab-ferment*, or rennet-ferment, is present, which possesses the property of quickly developing lactic acid out of lactose or sugar of milk. This ferment seems to be most abundantly produced in infants, and its activity may be estimated when it is stated that 1 part of rennet-*ferment* can precipitate 800,000 of casein. It acts in acid, in alkaline, and in neutral solutions of casein. The casein precipitate from milk by rennet differs from that thrown down by acids. Rennet is in common use in the manufacture of cheese.

Meat is quickly broken up into detached fragments by the solution of the connective tissue between the fibres; the transverse striæ become very distinct, the clear striæ dissolve first, and finally the whole disappears. Beef is more digestible than mutton, whilst veal and pork digest slowly. The flesh of young animals digests more rapidly that that of old ones, and lean meat quicker than fat. Cooking, by softening the tissues, favours digestion. Fibrous tissues, as tendons and ligaments, dissolve with a rapidity proportioned to their firmness, and even cartilage is slowly acted on. Gelatin, which is obtained by boiling the tendons, skin, and other connective tissues, is dissolved in gastric juice, and converted into a kind of peptone. It loses its power of gelatinising.

Action of the gastric juice on other constituents of food.—Gastric juice has no action on the *oils and fats;* but it is capable of dissolving the

connective tissue uniting fat cells into lobules, and of dissolving also the walls and protoplasm of the fat cells, thus setting the contained oil-globules free.

Starch is also unacted on by the gastric juice, but it is said to convert the erythro-dextrin and achroo-dextrin resulting from the action of saliva on starch into glycose. *Cane sugar* is gradually converted into grape sugar.

Conditions interfering with gastric digestion.—If a large excess of food be taken into the stomach, imperfect digestion takes place, and the partially-dissolved products are apt to excite irritation throughout the whole length of the alimentary canal. The presence of unwholesome or indigestible material leads to the secretion of an excess of acid and gastric derangement. Raw fruits of close texture, as apples, preserved fruits (as candied lemon and orange-peel), raw turnips and carrots, though they may be eaten with impunity when violent exercise is taken and the supply of more appropriate food is insufficient, yet, when given to children, are a fertile source of disorder. The consumption of alcohol, except in elderly people, is unnecessary, if not harmful. It is useful when the quantity of food is insufficient, and well-matured wine is probably the best form in which to take it. Large quantities impede, or may altogether arrest, digestion.

It has been found that the ingestion of large quantities of sugar impairs digestion, by causing the secretion of mucus, which acts injuriously in two ways: first, by preventing the gastric juice from becoming incorporated with the food, and secondly, by interfering with the absorption of that which is absorbed. Lastly, it may be remarked that, for proper digestion to be effected, a short period of repose should be permitted after a meal. Exercise, whether of the mind or body, interferes with digestion, by

withdrawing to the brain or muscles a portion of the blood that should be engaged in supplying the materials for the digestive process.

The stomach contains more or less gas, partly derived from air swallowed with the food and saliva, partly generated during the process of digestion. In one specimen, obtained from a dog five hours after feeding, 100 volumes contained CO_2 25·2, N 68·68, O 6·12.

Movements of the stomach.—The movements of the stomach have been chiefly observed in animals, though occasional opportunities have presented themselves in man, after injuries and in cases of extreme atrophy. They are effected by unstriated muscular tissue, so disposed as to form an external layer of longitudinal fibres, an internal layer of circular fibres, which is greatly developed at the cardiac and still more at the pyloric orifices, and of an intermediate layer of oblique fibres, occupying the cardia. When empty, the stomach is probably at rest, but soon after food is ingested movements commence. In the earlier periods of digestion, general contraction and shortening of the muscular fibres occur, the walls of the stomach equably compressing the food that has been introduced; but, after a time, contraction and relaxation succeed each other alternately, the contractions sometimes travelling in an undulating manner along the walls, whilst at other times deep constrictions are formed, almost separating the contents into separate portions. This often occurs near the middle of the stomach, or about three or four inches from the pylorus, the constriction that occurs at this point giving the stomach an hour-glass form. The wave of contraction usually passes from left to right, and is then termed "peristaltic"; sometimes in the opposite direction, and is then termed "anti-peristaltic." The movements are not very

energetic or rapid until towards the close of chymification, when the contents of the stomach have partially entered the duodenum, and they are best marked along the greater curvature. A peristaltic wave occupies about a minute in travelling from one end of the stomach to the other. The intervals between successive waves vary, but are shorter towards the close of digestion. Movements have been observed to take place after death. By some observers, as Brinton, the anti-peristaltic movement is denied, and the recurrent movement of the contents of the stomach, which undoubtedly occurs, is explained by considering that the peristaltic action of the gastric walls forces towards the pylorus the food in contact with them, but, the pylorus being closed, a reversed axial current is produced, the presence of which has led to the admission of an anti-peristaltic movement.

Influence of the nervous system on the stomach.—The stomach is supplied by the vagus and by the sympathetic nerves. The vagus contains fibres derived from the spinal accessory, which is a motor nerve. The evidence in regard to the effects both of section and of stimulation of the vagus on the movements of the stomach is unsatisfactory, and even contradictory, perhaps owing to different periods of digestion having been selected, and in part also to different animals having been chosen for experiment. Many observers have noticed paralysis of the stomach after division of the vagus; but others have seen some movements continue, or even that they have been as vigorous as before. Stimulation of the vagus by means of electricity causes contractions of the stomach to occur in the course of five or six seconds, especially during full digestion; but, when the stomach is empty, the contractions induced are feeble, or they may be altogether absent. Movements of the stomach have also been noted after stimulation of the two

sympathetic nerves in the neck, the first thoracic ganglion and the solar plexus. Stimulation of the corpora quadrigemina and optic thalami in some instances excites gastric movements. Destruction or removal of the brain and spinal cord renders the stomach more irritable. The splanchnic nerve is thought to be the inhibitory nerve of the stomach. Direct irritation of the stomach, as by scratching, pinching, or the application of irritants, only causes local and limited contractions. Opium inhibits the movements of the stomach. When distended, the stomach is subject to considerable passive movements, through the action of the diaphragm, and even of the heart.

Self-digestion of the stomach.—After death, if this has taken place during the digestion of food, it is not uncommon to find a large ragged orifice with them, and softened edges in some part of the wall of the stomach. In some instances the contents of the stomach have been found in the peritoneal cavity. Perforations of this kind are due to the action of the gastric juice secreted during life upon the dead walls of the alimentary canal. During life no action of this kind takes place, because the blood is rendered more alkaline in the vessels where the acid juice is secreted, and also brings with it the materials for nutrition. The mere circumstance of the stomach being part of the living body will not alone account for its resisting the action of the juice in ordinary digestion, for Bernard showed in a remarkable experiment that gastric juice is capable of digesting living as well as dead tissue, for he inserted the leg of a living frog through a gastric fistula into the stomach of a dog, and found that it underwent ordinary digestion. It may perhaps be stated generally that as long as living blood circulates in the tissues at normal pressure, the gastric juice is incapable of acting on them, but when normal

nutrition ceases, either in consequence of the formation of embola, or of ligature of vessels, and necrosis of tissue occurs, the gastric juice will exert its full action upon it. Ewald found that division of the cervical or upper dorsal region of the spinal cord, an operation that materially reduces blood pressure, caused, in the course of thirty-six hours, the formation of numerous circular clearly-defined lenticular ulcers without any trace of inflammatory processes.

Chyme.—The product of gastric digestion is termed chyme, and on ordinary diet is a whitish or creamy acid fluid, which passes through the pylorus as it is formed, and enters the small intestine. It contains:

1. The products of digestion up to the pylorus: peptone, dextrose, lævulose, peptonised gelatin.

2. All matters in a state of minute subdivision, but which are only partially acted upon by the saliva and gastric juice, such as raw starch and gum, the denser connective tissues, gelatin that is merely dissolved, some forms of albumin, and isolated and partially-digested muscular fasciculi.

3. Substances quite unchanged by saliva and gastric juice, such as cellulose, fats, and the fatty acids.

4. The fluid solutions and salts not as yet absorbed in the stomach, such as those of sugar, the vegetable acids, and the gastric juice itself.

The really insoluble and indigestible residue of the food remains for some time in the stomach, but is ultimately propelled through the relaxed pylorus by the peristaltic action of the stomach.

INTESTINAL DIGESTION.

As soon as the chyme enters the duodenum it is subjected to the action of three fluids, the bile, the pancreatic juice, and the secretion of the glands of the mucous membrane of the intestine. It has been

ascertained by means of experiments outside of the body that the admixture of the acid chyme with the alkaline bile causes precipitation of the peptones, the biliary acids being set free by the superior affinity of the gastric juice for the soda with which they are combined; but as soon as the alkaline pancreatic juice is added to the fluid, resolution of the peptones occurs, and the pancreatic ferments are enabled to operate. Some observers, however, deny with Dalton that any precipitation of the peptones occurs within the body.

Formation of the bile.—The bile is formed continuously by the cells of the liver, and is in part conducted to the intestine by the ductus communis choledochus, and in part accumulates in the gall bladder, from which it is discharged in considerable quantity soon after food is taken.

Characters of the bile.—The bile, whether extracted immediately after death from man, or obtained by means of a biliary fistula in animals, is a yellow, brown, or greenish fluid, presenting dichroism and some degree of fluorescence, with sp. gr. 1020, of ropy consistence and bitter taste. Its reaction is alkaline. It contains, as its principal ingredients the taurocholate and glycocholate of soda, which are present in the proportion of from 2 to 10 per cent. Besides these peculiar biliary salts the bile contains 5 per cent. of ordinary salts, mucus, cholesterin, and lecithin, collectively. Water varies from 91 to 85 per cent. Finally there is a minute quantity of sugar, and sometimes of a diastatic ferment. The colour is due to the two colouring matters known as bilirubin and biliverdin. The colouring matter of the bile is probably a derivation of the colouring matter of the blood, hæmochromogen, and is itself in process of being decomposed into the colouring matter of the urine or urobilin. Bile assumes a green colour when a few drops of a watery solution of iodine are added to it.

Gmelin's test for the colouring matters of the bile.—Bile is rendered vivid green with fuming nitric or nitroso-nitric acid, a play of colours, from green to blue, violet, red, and yellow, being observed, due to the oxydation of the bilirubin.

The characteristic biliary salts.—These are formed by the combination of taurocholic acid and glycocholic acid with sodium. Both are present in human bile (Yeo and Herroun). *Sodium glycocholate* is abundantly present in the bile of herbivora; it exists in moderate quantity in the bile of omnivora, and is altogether absent in carnivora. Its formula is $C_{26}H_{42}NO_6Na$. It is soluble in water and in alcohol, but is insoluble in ether, whilst it is precipitated by both neutral *and* tribasic lead acetate. It may be prepared by evaporating bile to dryness, dissolving the sodium glycocholate out from the residue by means of absolute alcohol, decolorising with animal charcoal, and then adding a large volume of ether; a whitish precipitate falls, which, after a time, crystallises in star-shaped masses of fine radiating needles (Dalton). When boiled with alkalies or acids, it is decomposed with absorption of H_2O into glycine $C_2H_5NO_2$, and cholic acid $C_{24}H_{40}O_5$.

Sodium taurocholate is found in the bile of all animals. It exists alone in the bile of carnivora, and preponderates over the glycocholate in omnivora. Its formula is $C_{26}H_{44}NSO_7Na$. It may be obtained from bile in the same way as the glycocholate, like which it crystallises in needles, but from which it may be separated by the circumstance that it is not precipitated from its watery solution by the neutral, but only by the tribasic acetate of lead. On boiling with dilute acids or alkalies, it is decomposed with absorption of H_2O into taurine $C_2H_7NSO_3$, and cholic acid $C_{24}H_{40}O_5$. Both of the biliary salts exert a right-handed rotation on polarised light (Dalton).

Pettenkofer's test for the bile salts.—When existing in considerable quantity, the biliary salts are recognised by their solubility in water and alcohol, by their insolubility in ether, and their behaviour with the salts of lead; but it is often of importance to determine the presence of these salts in small quantities, and then the test devised by Pettenkofer is invariably used. In applying Pettenkofer's test, a drop of syrup containing one part of cane sugar dissolved in four parts of water is added to each cubic centimetre of the suspected solution. On the addition of a drop or two of strong sulphuric acid, the mixture begins to assume a cherry-red colour, which soon passes into violet. If the original fluid contain more than one part in 500 of the biliary salts, a precipitate of cholic acid occurs on the addition of the sulphuric acid, which, however, soon clears up, and after becoming violet, the mixture assumes a rich purple blue. Dalton, who has particularly investigated this subject, points out that various precautions should be taken to render the test a certain one, and, in particular, the liquid to be examined should be free from other organic substances, and from colouring matters, since olein, oleic acid, amyl, alcohol, albuminous matters, and the salts of morphia and codein, all give a red colour with a solution of cane sugar and sulphuric acid. The process above described for extracting sodium glycocholate should therefore be practised. The spectrum of Pettenkofer's test gives a wide and dark absorption band at the line E of the solar spectrum, near the junction of the yellow and the green, and the spectrum is short owing to the absorption of the whole of the violet and part of the indigo rays, and also of a portion of the red.

Quantity of the bile.—Dalton found, from examination of the fluids obtained from a duodenal

fistula, that the largest quantity of bile in a given time was discharged into the intestine immediately after food has been taken. The average quantity secreted per diem may be estimated at from 1 to 2 grammes (15 to 30 grains) per hour for every kilogramme of body weight, or about 1,500 grammes per diem (about 3 lbs. 3 oz.) for a man of average weight. In the dog the quantity is larger, amounting to about 20 grammes of bile containing 1 gramme of solids for each kilogramme of body weight per diem. It is increased with abundant animal food, and is diminished on fat and starch diet. The quantity of bile is greatly increased by certain drugs, and especially by podophyllin, corrosive sublimate, and sodium salicylate. The evidence that the bile is really formed in the liver rests on the facts (1) that ligature of the vena portæ at once arrests the flow of bile, though neither the blood of the vena portæ nor of the hepatic artery contains any of the biliary salts or colouring matters; (2) that after ablation of the liver the biliary salts do not accumulate in the blood, though they immediately begin to do so after ligature of the common bile duct.

Uses of the bile.—The uniformity with which the bile is discharged into the alimentary canal just below the stomach throughout the whole of the mammalia seems to indicate that it fulfils some important purposes in digestion, yet it has but little chemical action on either proteids or on starch paste raw or boiled, or on fats, though it aids in their emulsification or mechanical division. It contains a diastatic ferment, converting starch into sugar, but the action is feeble. If a biliary fistula be established and the bile allowed to flow from the body without entering the intestine, it is found that on ordinary diet serious disturbance of the functions of digestion and absorption ensue, the animal becomes thin, its hair falls off, and it dies apparently from debility.

Life can, however, be preserved for years if the food supplied is in large quantity. It is not, therefore, absolutely necessary. The chief uses that have been demonstrated are: 1. That bile moistens animal membranes, and permits oil or emulsions of oil to pass through them with facility; this property is not due to the alkalinity of the bile, for it is possessed by the pure biliary salts. The importance of this property in the process of absorption is great. 2. Bile, moreover, acts as a stimulant alike to the neuro-muscular and glandular apparatus of the walls of the intestines, increasing the peristaltic action and the secretion of intestinal fluids. Lastly, bile is an antiseptic. Hence, when bile is formed in insufficient quantity hunger is experienced, the bowels are costive, much gas is developed, and the fæces are pale and ill-smelling. In passing along the alimentary canal the biliary salts are decomposed, and the free taurin and glycine probably undergo reabsorption, for little or none of tauro-cholates and glyco-cholates are discharged with the fæces, though in the dog the fæces contain some cholalic acid, which may undergo further decomposition into dyslysin; and it is, perhaps, to the loss of sulphur by the œconomy that the ill effects of biliary fistulæ are partly due, the hair in particular being deprived of one of its most important constituents. The bilirubin is decomposed into biliprasin, which no longer gives Gmelin's reaction, and urobilin, which is the colouring matter of urine. The cholesterin is discharged by the fæces, but the lecithin is either decomposed or absorbed, for none of it appears in them.

The **pancreatic juice.**—The pancreatic juice is secreted intermittingly, and enters the alimentary canal by the same orifice as the bile. It is a thick transparent fluid, secreted sparingly, the quantity obtained from a fistula in a large dog during one act of digestion being only about one gramme or one gramme

and a half. It is colourless and tasteless, and has a strong alkaline reaction. It contains so much albumin that, on boiling, it coagulates, and its albumin is precipitated by all the mineral acids. The composition of the pancreatic juice is: Water, 90 per cent.; organic substances (albumin and ferments), 9; and mineral constituents, of which sodium chloride forms by far the greatest part, 1 part. The gland is most active two hours after food, then secretes more slowly, and again becomes more active about five to seven hours after the meal.

Uses of the pancreatic juice. — Though secreted in such small quantity, the pancreatic juice is one of the most important of the digestive fluids, for it contains three hydrolytic ferments: a peptone-forming ferment, *trypsin;* a fat-splitting ferment, *steapsin;* and a diastatic ferment, *amylopsin.*

1. *Action on albumins.*—Trypsin converts proteids first into alkali-albumin, and then into true peptones. This action of the trypsin of the pancreatic juice on proteids only takes place in an alkaline fluid, and is of a corrosive nature. The activity is dependent partly on the quantity of ferment, and partly on that of sodium carbonate contained in the juice. Beyond a certain point the addition of ferment causes no increase; with a medium quantity of ferment about 1 per cent. of sodium carbonate is most effective. Cubes of coagulated albumin subjected to the action of the juice do not swell up, as in gastric juice, but are slowly eaten away. If the action of the trypsin be continued on the peptones, about one-half becomes *antipeptone,* which is not capable of undergoing any further digestive changes, whilst the remainder is converted into the amido-acids, leucin and tyrosin, and, when the peptones are derived from fibrin and gluten, asparaginic acid appears. Still more protracted action leads to the formation of the fœtid substances named indol and

phenol. Put into a tabular form, the action of trypsin may be thus represented :

Albumin + trypsin + soda solution of 1 per cent. forms at the body temperature, first alkali-albumin, insoluble in water, and then

	Hemipeptone.		Antipeptone.
Normal digestive products.	Leucin	Indol.	Putrefactive products.
	Tyrosin	Phenol.	
	Hypoxanthin . .	Fatty acid.	
	Asparaginic acid .	Ammonia.	
	Glycocoll . . .	Sulphuretted hydrogen.	
		Hydrogen.	
		Carbonic acid.	

The trypsin seems to be formed at the expense of a mother substance, named by Heidenhain *zymogen* substance, the development of which has been carefully studied. The acini of the glands are lined by cells, and in each cell, just before digestion, three regions or zones are recognisable, a basal or *peripheric* zone near the attached extremity, which is homogeneous, free from granules, and which stains with carmine; a *median* zone, occupied chiefly by the nucleus; and an *internal* zone at the free extremity, which is granular, and does not stain with carmine. Soon after digestion commences, when secretion is most active, the internal zone, at first large, becomes smaller and more granular, whilst the peripheric zone augments, and ultimately almost fills the cell, the median zone, with the nucleus, remaining unaltered. As the secretion becomes less active, the internal granular zone reforms at the expense of the peripheric zone. Thus, during secretion, the material which has been gradually forming in each cell, and which has accumulated near its free extremity, is discharged, whilst new matter is taken up from the blood by the

protoplasm at the base of the cell, to be elaborated in the interval of digestion. If the *pancreas* taken from the living animal be extracted with glycerin, the glycerin extract does not act on proteids, and only contains traces of trypsin, but it does contain the zymogen substance, which is believed to be a combination of trypsin with a proteid, and the trypsin is set free by the mere presence of water at a moderately high temperature, of weak acids, or of oxygen, whilst its separation is retarded by sodium chloride, and by the alkaline carbonates. If, instead of the pancreas, the pancreatic juice is extracted with glycerin, no zymogen substance is obtained, but the trypsin itself. Hence at the moment of secretion zymogen ferment is converted into trypsin. The largest quantity of zymogen is found fourteen hours after food.

2. *Action on fats.*—Pancreatic juice exerts a double action on fats; it first converts them into an emulsion, and then decomposes them with the absorption of water into glycerin and the fatty acids. Two grammes of pancreatic juice are required to emulsionise one gramme of fat. After complete decomposition by the agency of the steapsin, the fatty acids form soaps with the alkali of the juice and of the intestinal fluid

3. *Action on starch.*—The action of the pancreatic juice on starch resembles that of saliva, though it is much more energetic, the amylopsin it contains acting not only on boiled but on raw starch, converting each into dextrin and grape sugar.

The extirpation of the pancreas, or the ligature of the duct of Wirsung, or the obliteration of this duct by means of injections, are operations that appear to be well borne by mammals; but in pigeons the processes of digestion are so seriously interfered with that death invariably occurs.

Innervation of the pancreas.—There appears to be a centre controlling the secretion in the medulla

oblongata; the nerves proceed from the splenic, hepatic, and superior mesenteric plexuses, but the nervous circle is not accurately known. Induction currents applied to the gland induce secretion. The secretion of the gland is arrested by atropine. It is discharged under a pressure of about 17 mm. Hg.

Movements of the small intestine.—The arrangement of the longitudinal and circular layers of muscular fibre in the walls of the intestine enable it to execute peristaltic movements, the effect of which is to propel its fluid or pulpy contents from above downwards with more or less rapidity. These waves of contraction are excited by the presence of food, which stimulates the sympathetic fibres, and then acts through reflex centres situated in the sympathetic ganglia and in the spinal cord, but the precise nervous circle has not been accurately ascertained. A powerful *inhibitory* influence on the intestinal movements is exerted through the *splanchnic* nerves. Stimulation of these nerves causes vascular contraction and anæmia, with inhibition of the movements, whilst section of the nerve causes congestion of the intestinal vessels and increased peristaltic action. Under certain circumstances, as when there is much food in the intestine, stimulation of the *vagus* excites peristaltic action.

Peristaltic movements may be induced or intensified by the direct action of electrical currents, by mechanical irritation, by cold, and by the application of concentrated saline solutions. Also by all circumstances increasing the venosity of the blood circulating in the intestine, such as general asphyxia, pressure on the aorta, ligature of the mesenteric arteries, and lastly by nicotin. Muscarin, caffein, and most purgatives, morphia, and belladonna, have an opposite effect (Frédéricq).

Function of the glands of the small intestine in digestion.—The walls of the small intestine

contain two sets of glands: the glands of Brünner, chiefly or exclusively found in the duodenum, and the glands of Lieberkühn, which are closely arranged in the mucous membrane in its whole extent. The secretion of the *tubular and convoluted glands of Brünner* appears to resemble that of the pancreas in containing a diastatic ferment capable of converting starch into sugar; and a glycerin extract of the upper part of the duodenum, where these glands are most abundant, yields a ferment which dissolves fibrin easily. The secretion of *Lieberkühn's follicles* can best be obtained by a Thiry's fistula, which is thus made: an excised piece of intestine, still connected with mesentery, is ligatured at one end, while the other is united with the abdominal wound. The continuity of the intestine is repaired by carefully sewing the ends together. An alkaline opalescent fluid is obtained, which, according to some authors, acts, like the pancreatic juice, upon all the constituents of the food, proteids, fats, and carbohydrates. The use of the *valvulæ conniventes* is not only to present a larger surface for absorption, but to delay the progress of the food, and thus enable the digestive process to be conducted more slowly and perfectly.

Changes of the chyme in the small intestine.—The chyme (described at page 189) becomes alkaline or neutral in the jejunum, owing to admixture with the biliary, pancreatic, and intestinal secretions, but in the ileum it again becomes acid from the formation of acids consequent on the putrefaction of proteids and upon fermentation processes. Thus: Pepsin and trypsin acting on albumin + $n(H_2O)$ yield peptone, leucin, tyrosin, xanthin, asparaginic acid. Steapsin acting on fats converts tristearin into glycerin and stearic acid; $C_{57}H_{110}O_6 + 3(H_2O) = C_3H_8O_3 + 3(C_{18}H_{36}O_2)$. Lactic ferment acting on milk sugar converts it into grape sugar, and this into lactic acid;

$C_{12}H_{22}O_{11} + H_2O = (C_6H_{12}O_6) = 4(C_3H_6O_3)$. Butyric ferment acting on lactic acid yields butyric acid + carbonic acid and hydrogen; $2(C_3H_6O_3) + 2(H_2O) = C_4H_8O_2 + 2(CO_3H_2) + H_4$.

Unknown ferments convert taurocholic acid into taurin and cholic acid—$C_{26}H_{45}NSO_7 + H_2O = C_2H_7NSO_3 + C_{24}H_{40}O_5$; cellulose into carbonic acid and marsh gas —$n(C_6H_{10}O_5) + n(H_2O) = 3n(CO_2) + 3n(CH_4)$; albumin + $n(H_2O)$ into globulin, peptone, and leucin, tyrosin, xanthin, indol, phenol, skatol, fatty and carbonic acids, ammonia, sulphuretted hydrogen; glycerin $C_3H_5(OH)_3$ into $H + CO_2$ + succinic acid + fatty acids; malic, tartaric acids into butyric and acetic acids with evolutions of CO_2.

Amongst the final products of the putrefactive decomposition of non-azotised substances after the oxygen in the intestines is consumed are CH_4, or marsh gas, and CO_2. The contents of the small intestine begin to assume the appearance and consistence, and to give the odour of, fæces, in the lower part of the ileum.

Digestion in the large intestine.—The contents of the large intestine are usually acid in the upper part from lactic acid and other fermentations, and by far the larger portion of the nutritive materials of the food have been absorbed in the lower part; they gain in consistence, and are more or less periodically discharged as fæces. The *fæces* consist (1) of elastic tissue, woody fibre, the husks of grain, and fragments of most of the constituents of the food which have been hurried on before being thoroughly incorporated with and digested by the gastric and other fluids. (2) Of the products of disintegration of the biliary colouring matters. (3) Of unaltered mucin and nuclein. (4) Of combinations of fatty acids with lime, especially after milk diet. (5) Of salts, especially those which diffuse with difficulty, as the ammoniaco-magnesian phosphate and

phosphate of lime. According to J. Munk, human fæces contain from two to ten per cent. of albuminoids contained in food of animal origin, such as meat, eggs, and milk, fifteen per cent. of albumin of leguminous plants, fifteen to thirty per cent. of the albumin of rice, bread, and potatoes. Starch is almost completely digested, only about one per cent. appearing in the fæces; and fat is almost completely absorbed, only five per cent. reappearing, unless the quantity ingested have been unusually large. The quantity of the fæces discharged per diem is on the average 170 grammes (about 3,000 grains). It is greater, and the fæces are less offensive on vegetable than on animal diet. They contain 75 per cent. of water. The fœtid odour is due to indol and skatol.

Fate of the ferments.—Of the various ferments which proceed from the salivary, peptic, pancreatic, and intestinal glands, and which in the aggregate must amount to a considerable quantity, very little escapes from the body either by the urine or the fæces; and evidence has been adduced by Langley, which seems to show that the amylolytic ferment produced by the salivary glands is destroyed by the hydrochloric acid of the gastric juice; that the proteolytic and rennet ferments generated by the gastric glands are destroyed by the alkaline salts of the pancreatic and intestinal juices, and by trypsin, and that the proteolytic and amylolytic ferments produced by the pancreas are not improbably destroyed in the large intestine by the acids there formed.

Gases of the alimentary canal.—These partly consist, in the stomach, of nitrogen of air that has been swallowed with the food, and partly of carbonic acid gas evolved during processes of fermentation. The oxygen of the air that is swallowed is soon absorbed. In the lower part of the alimentary canal nitrogen again forms the principal constituent of the gases

found in this region, but there are also considerable quantities of hydrogen and carbonic acid gas. In some cases marsh gas has been found in the proportion of 50 per cent. or more of the total quantity of gas.

Defæcation.—The lower outlet of the alimentary canal is guarded by a sphincter, which preserves a state of persistent contraction, sometimes named its *tone*, which is evidently due to the constant influence of the spinal cord; since, if this be destroyed, relaxation of the muscular tissue occurs, and the contents of the bowel are discharged. The sphincter is partly formed of striated muscular tissue, and is to some extent under the influence of the will, but is chiefly composed of unstriated muscle, which is altogether withdrawn from voluntary control. The nervous mechanism is complicated. The stimulus is the presence of fæces acting on *afferent* fibres distributed to the mucous membranes and muscular coat of the rectum, which conduct impulses to the *anospinal* centre, situated in the lumbar region of the cord; from this, *efferent* fibres conducting motor impulses proceed to the unstriated muscles of the intestine, and increased peristalsis results. But this is not all. The expulsion of the contents of the rectum must be preceded by the relaxation or inhibition of the sphincter, and there must therefore be an inhibitory centre. The experiments of Ott show that centres inhibiting the anospinal centre are situated in the base of the thalami and the upper end of the crura cerebri; the fibres run in the middle third and internal half of the lateral columns of the cord. They appear to decussate, the highest point of decussation being in the pons, and the lowest point being about half an inch below the apex of the calamus scriptorius. Under ordinary circumstances the abdominal muscles act but slightly, and then by an exertion of the will; but if the stimulus be violent, strong motor impulses may

radiate to the abdominal muscles, which then act spasmodically and involuntarily, just as in parturition. In diarrhœa, with involuntary discharge of fæces, the voluntary control over the external sphincter is lost, and the stimulus excites the anospinal centre too powerfully for the internal sphincter to resist, whilst the abdominal muscles often contract with great violence. The discharge of the fæces usually takes place once or twice in 24 hours. Irregularity in the performance of this function leads to many troubles.

Absorption of the food.—The object of the digestive process is to render the insoluble substances taken as aliment soluble; in other words, to convert colloids, such as albumin, gluten, and gelatin, into crystalloids, such as the peptones; and the conditions that exist in the alimentary canal are well calculated to favour the diffusion of these substances into the blood and lymph. In the intestine is a slowly-moving fluid, charged with diffusible or crystalloid materials, sugars and peptones, whilst in the walls of the intestine are two systems of vessels, the blood-vessels and the lymphatics, both of which contain albumin and colloidal substances moving with considerable rapidity. A current is accordingly established from the intestine towards the blood-vessels, which, it is known, take up and carry off, both from the stomach and the intestinal canal, a large proportion of the products of digestion. The absorption of the fats, however minutely we may conceive them to be divided, is more difficult to explain. It has generally been held that it is effected by the protoplasm of the columnar cells, which invest the villi, aided, perhaps, by the movements of the rods which form the striated border. Some recent investigations, however, seem to show that it may be in part due to amœboid cells which lie at the bases or attached extremities of the columnar epithelial cells of the villi and intestinal mucous membrane, and

send up long processes between the cells to the surface, where they seize upon and ingest the passing particles of fat, and conduct them to the commencement of the lymphatics, here called lacteals.

CHAPTER VIII.

CHYLE AND LYMPH.

The **chyle and lymph.**—These fluids may be considered together, since they are contained in the same system of tubes, and only differ from each other at certain periods. During fasting they are alike, but when digestion is in progress the lymphatics distributed to the intestines and abdominal viscera become charged with the products of digestion, and their contents are materially modified both in aspect and in chemical composition.

Properties of the lymph.—Lymph is clear and transparent, contains albumin, and, after passing through a gland, or perhaps even before, lymph corpuscles. It is capable of feebly coagulating, and of setting into plasma and clot.

Derivation of lymph.—*Lymph plasma* is believed to be the superfluous fluid part of the blood which has escaped from the blood-vessels, and which has irrigated the tissues and ministered to their nutrition. The salts it contains correspond nearly with those of the blood plasma. It is, however, a more watery fluid, the albumin being reduced to about one-half and the fibrin generators to two-thirds of the quantity in which they exist in the blood. It is probable that it contains some of the products of the waste of the tissues.

The **lymph corpuscles.**—The corpuscles, or morphological elements of the lymph, resemble the white corpuscles of the blood, and they are derived (1) from the corpuscles which are so abundant in the tissue of the lymphatic glands; (2) from the adenoid tissue of other parts of the body, as the mucous and submucous tissue of the intestinal tract, the spleen, and the marrow of bones; (3) some may also be true white corpuscles of the blood which have wandered into the lymphatic system, especially when that system invests the blood-vessels as with a sheath; (4) and some, lastly, may originate from the fission or division of previously-formed lymph corpuscles.

Properties of chyle.—The fluid absorbed by the lymphatics of the intestine during digestion is termed the "chyle," or "lacteal fluid," because it presents, especially when much fat has been contained in the food, a milky aspect. It is an alkaline fluid, with a sp. gr. of 1012—1022. It contains sugar, and albumin in the form of peptone and salts in solution, and fat molecules in suspension or in the state of emulsion. In addition, even in the villi, there are a few lymphoid cells, and these increase in number after the chyle has passed through one or more of the lymphatic glands of the mesentery. In these glands a process of elaboration or assimilation takes place, as a result of which the proteids absorbed are converted into fibrin generators. Hence the chyle taken from one of the more centrally situated lacteals, or from the thoracic duct itself, where it is mingled with the lymph coming from other parts of the body, is capable on standing of coagulation, separating into a soft and easily-broken clot and a plasma. In the upper part of the thoracic duct, corpuscles, presenting the character of red blood-corpuscles, are found, which, however, have probably escaped from the vascular system and entered the lymphatic system of the spleen, or other

abdominal organ, under the greatly increased venous pressure attendant upon digestion.

Quantity of the chyle.—The chyle enters the circulation through the thoracic duct intermittently. The quantity is large with ordinary diet, an hour or two after digestion has commenced, and sooner if such an emulsion as milk be taken; and it is estimated that the constant and more equable supply of lymph from the body generally, and the variable supply of chyle from the digestive organs, each constitute about one-half of the fluid traversing the thoracic duct. The absolute quantity is very large. In one case, six kilos or about 13 lbs. of lymph were obtained in twenty-four hours from a fistula in the thigh which opened into a large lymphatic.

Movement of the chyle and lymph.—The onward current of the chyle is maintained:

(1) By the contraction of the layer of unstriated muscular tissue in the villi, which, aided by the valves in the larger lacteals, act like so many little force-pumps, driving the fluid absorbed into the central lacteal onwards to the subjacent tubes.

(2) The current thus established will be increased in those lymphatics which form sheaths around blood-vessels by any dilatation of these blood-vessels, the backward current being prevented by valves, whilst there will be under these circumstances an increased quantity of interstitial fluid.

(3) In a similar manner, increased blood-pressure in all parts of the body will, by causing increased filtration through the blood-vascular walls, lead to more rapid flow of lymph.

(4) The act of inspiration is a *vis a fronte*, which draws the lymph contained in vessels outside the chest into the vessels within the chest, the opposite effect of expiration being neutralised by the valves.

(5) A powerful agent is the rapid current of

venous blood over the mouth of the opening of the thoracic duct into the angle of junction of the jugular and subclavian veins.

(6) The last cause to be mentioned which accelerates the onward current of lymph is the contraction of the lymphatics themselves, aided again by the valves. These contractions are not much accentuated in man and the higher animals; but in the amphibia, and some fishes, the muscular tissue by which it is effected is collected into definite regions, forming true lymphatic-hearts, which contract rhythmically and propel the lymph with considerable vigour. The rate of movement in the chief cervical duct of the horse is estimated at about one foot per minute. The lateral pressure in the thoracic duct of the horse is about 1·2 mm. Hg.

The nervous system acts on the lymph current through its distribution to the smooth muscular fibres of the lymphatics.

CHAPTER IX.

GLYCOGENIC FUNCTION OF THE LIVER.

Glycogen.—This substance, named also hepatine, and bernardine, and zo-amyline, is widely distributed. It is found in all developing animal cells and nerves, in embryonal tissues, and in the villi of the chorion; in colourless blood-corpuscles, in the muscles, and especially, where it was first recognised by Bernard, in the cells of the liver, where it exists in an amorphous condition. Bernard believed that this substance, derived from the food and elaborated in the liver, was converted in that organ into sugar by the aid of a ferment. The sugar thus formed, he thought,

immediately entered the circulation and underwent oxydation. Pavy has, however, shown that no sugar is contained in the blood returning in the hepatic veins from the liver to the heart during life, and that it only makes its appearance in this blood after (though, it must be admitted, very quickly after) death.

Mode of obtaining glycogen. — Bernard's method was as follows:—Cut up a portion of liver recently removed from an animal into small fragments, and throw them into boiling water; pound in a mortar, and boil for a quarter of an hour in a little water; pass the fluid through a linen cloth, adding to it some animal charcoal. To the opaline fluid thus obtained, add four or five times its volume of alcohol at about 40° C. (100° F.), when glycogen is precipitated. This must be well washed with alcohol. It may be further purified by boiling with caustic potash, precipitating with alcohol, and removing any adherent potash with acetic acid.

Brücke's method is to throw the liver into boiling water; then, when hardened, to pound it in a mortar, and boil the mass for half an hour in water. The milky liquid is decanted, and fresh water added as long as it acquires an opaline tint. These liquids are put together, refrigerated and filtered, and then there are added alternately hydrochloric acid and mercuro-potassic iodide as long as a precipitate, consisting of albuminous compounds, falls, and the fluid is filtered. The filtered liquid is treated with alcohol, which precipitates the glycogen. This may then be collected and purified as usual.

Chemical composition and properties of glycogen.—The composition of glycogen is expressed by the formula $C_6H_{10}O_5$, and it is therefore isomeric with starch and dextrin. It is a white powder without smell or taste, insoluble in alcohol and ether, but dissolving in boiling water, and forming an

opalescent fluid, which rotates the plane of polarised light strongly to the right. On the addition of an alkali the opalescence disappears; with ioduretted potassium iodide it gives, not a blue colour like starch, but a red colour, which disappears with heat, and reappears on cooling. It does *not* reduce the oxide of copper in an alkaline solution of copper sulphate, which distinguishes it from glycose. It is precipitated by lead acetate, which distinguishes it from dextrine; when boiled with acids it is converted into achroo-dextrin and ptyalose, and it undergoes a similar change with the animal ferments, ptyalin and amylopsin.

Quantity of glycogen contained in the liver.—In health the liver always contains glycogen, the quantity varying from about $1\frac{1}{2}$ to $2\frac{1}{2}$ per cent. of the weight of the liver in man. The proportion differs in other animals. In the case of the fowl it has been known to rise to 12 per cent. It seems to be chiefly stored up around the nucleus in the cells in relation with the hepatic vein.

Influence of food on glycogen.—The first and most important factor is the food. If a dog be supplied, in addition to its proper food of proteids and fat, with a considerable quantity of *starch*, *sugar* of almost any kind, such as cane, grape, milk, fruit sugar, or glycerin, a large accumulation of glycogen takes place. Mannite and inosite, however, and gum, do not increase it. The addition of fats and soaps to the ordinary food causes no increase. The effect of a free supply of proteids, even if starch and its congeners be withdrawn from the food, is to maintain a moderate formation of glycogen in the liver. Gelatin does not conduce to the production of glycogen.

Prolonged fasting leads to its total disappearance.

Influence of the nervous system on glycogeny.—It has been found by experiment that lesion of the floor of the fourth ventricle near its

lower part produces diabetes or saccharine urine. But this part of the medulla oblongata is the centre of the hepatic vaso-motor nerves, and lesion of these nerves in any part of their course from the medulla oblongata to the liver, whether in the spinal cord or in the sympathetic cord, also leads to diabetes. The explanation that is offered is, that such lesions as those just referred to seriously interfere with the circulation through the liver, the calibre of the vessels is altered, the current of blood moves at a slower rate, and the liver becomes charged with sugar because the blood ferment has now time to act on the glycogen and effect its conversion into that substance. But the sugar diffuses easily into the blood, and is immediately filtered off by the kidneys, rendering the urine secreted saccharine. Section of the splanchnics prevents the occurrence of diabetes after puncture of the floor of the fourth ventricle, and even if diabetes has been induced by this means it arrests its production. The reason of this is that section of the splanchnics causes such an immense accumulation of the blood in the portal vessels and abdominal viscera, that the liver is rendered anæmic, and hence no sugar is formed in it.

Influence of drugs on glycogeny.—A variety of drugs, which are capable of paralysing the vaso-motor nerves of the liver, act like puncture of the floor of the fourth ventricle, and by retarding the current of blood through its vessels lead to an accumulation of sugar in its cells, and secondarily to diabetes. Such are curare, when artificial respiration is not maintained; chloroform, ether, chloral, and amylnitrite.

The *ferment* to which reference has been made is considered to be present in the blood.

Mother substance of glycogen.—There seems to be strong reasons for believing that glycogen may

be derived directly from the carbohydrates of the food to which it is, in its chemical composition, so closely allied; it may, however, also be derived from taurin and glycin; the latter substances splitting into glycogen and urea. Its increase on abundant flesh diet renders it probable that the albumins can be broken up into a non-nitrogenous portion, glycogen and a nitrogenous portion.

Destination of glycogen.—Pavy and others believe that during life no conversion of glycogen into sugar takes place, or at least that there is no evidence of such conversion, but most experimenters are of opinion that sugar is being constantly formed from glycogen in small quantities, and is taken up by the hepatic venous blood, which is known to be richer in sugar than ordinary blood, and that it is applied either to the production of heat, or to the development of muscular force by oxydation.

Functions of the spleen.—The functions of the spleen are obscure. It is believed to be a place where red blood-corpuscles are broken down, and also one where white corpuscles are formed. It is evidently an important organ, for it receives a large supply of blood; it undergoes great changes in volume; it executes slow rhythmical movements of contraction and expansion. The relations between the small arteries and veins are peculiar, the intermediate channels being of the nature of lacunar spaces rather than of capillary vessels; and the circulation in the spleen is peculiar, in the circumstance that the force driving the blood through the vessels is not so much derived from the heart as in other organs; but is due in part to a rhythmic contraction of the unstriated muscles existing in the capsule and trabeculæ of the organ. Each rhythmic contraction with the succeeding expansion lasts in dogs about one minute (Roy). The muscular fibre cells of the spleen can be made to contract by

stimulation of a cut sensory nerve, or of the medulla oblongata, or of the peripheric extremities of the cut splanchnics and vagi through which the motor impulses seem to pass. On the other hand, the spleen may be extirpated, both in animals and in man, without serious result, the chief effect which has been observed being hypertrophy of the lymphatic glands and of the red marrow of bones; and it is reasonable therefore to conclude that the hypertrophied tissues discharge a vicarious function, and this is probably the production of lymphoid and white corpuscles. Little information in regard to its functions can be obtained from examination of the blood going to and returning from it, but, such as it is, it seems to show that white corpuscles have been added to it. In diseases, again, in which the spleen is much enlarged, as in ague, the blood is found to contain an excess of white corpuscles, a condition that is named leucæmia. The splenic arterial blood in one case contained one white to 2,200 red corpuscles, whilst in the blood of the splenic vein the proportion was one to sixty. Chemical examination of the splenic pulp affords support to the view that red corpuscles are broken down in the spleen, for it contains many of the products of their regressive metamorphosis, as pigment, leucin, xanthin, hypoxanthin, and albuminous compounds rich in iron; inosite; cholesterin; and lactic, acetic, formic, butyric, uric, and succinic acids. Moreover, under the microscope large masses of protoplasm are found containing red corpuscles, more or less discoloured, to the number of ten or more.

The rhythmical contractions of the spleen, as shown in tracings taken with plethysmograph, occur in the cat and dog at intervals of about one minute.

Functions of the thymus and thyroid body. — These organs, sometimes included with the suprarenal bodies under the general title of the

ductless glands, seem to be remains of organs which may once have been of importance in the œconomy, but which, in the process of evolution, have come only to play a subsidiary part. This view is suggested by the temporary activity of the thymus, which attains its largest size about the end of the second year of life, and then gradually atrophies. It is thought that both the thymus and the thyroid body may minister to the formation of the white corpuscles of the blood. The chemical composition of their expressed juice resembles that of the spleen. As in the case of the spleen, many different views have been entertained in regard to the function of the thyroid, the following being the most important: 1. That it is a blood regulator for the upper half of the body, and especially for the brain, so that when this is likely to be suddenly rendered anæmic, as on assuming the erect posture after long lying, it surrenders blood to it; and on the other hand, when the brain is likely to be surcharged, as the result of increased action of the heart, it becomes distended with blood. It may also act in another way when thus distended by compressing the carotids, for it has been observed that when very violent muscular efforts are made the carotids are pulseless. 2. That it is a blood-forming gland. 3. That it aids in regulating the voice. 4. That it is a respiratory organ. 5. That it fulfils a simply mechanical function, and is simply an elastic cushion, protecting the subjacent parts from injury. The suprarenal capsules receive a remarkable nervous supply, but their use is unknown.

CHAPTER X.

THE FUNCTIONS OF THE SKIN.

The skin, by its elasticity, its density, and toughness, protects the subjacent parts from injury; the desquamation or scaling of the surface, which is constantly taking place, preserves to a certain extent its cleanliness, and enables the body to throw off adherent particles of a harmful nature, such as the spores of fungi, thorns, and the like, which may have accidentally implanted themselves in or on its surface. Secondly, the rich supply of nerves in its tissue renders it a highly efficient sensory organ, the impressions it receives being termed, from their wide distribution, those of *common* sensation, whilst the long outrunners that it possesses in the form of hairs, and the exquisite sensibility of their bulbs, convey to the mind important information of the approach of a foreign body. Thirdly, the immense capillary network of blood-vessels that ramifies in its substance renders it an important agent in the regulation of the heat of the body; for when the capillaries are contracted the bad conducting power of the dermis and epidermis for heat preserves the internal temperature at a high standard, whilst, when the capillaries are dilated, the blood they contain is drawn from the deeper-seated and warmer parts of the body, and loses much heat by conduction, radiation and evaporation. Fourthly, the skin is an efficient organ of secretion, giving off water charged with various soluble substances, and oily material. Lastly, it absorbs O and eliminates CO_2, and plays therefore a subsidiary part in the function of respiration.

The **cutaneous respiration.** — In man and the higher animals the part played by the skin in respiration is quite subsidiary to that of the lungs, but in the frog it is so important that life can be preserved even after the lungs have been removed. The quantity of *oxygen* absorbed by the skin as compared with that by the lungs is as 1 : 127. The quantity of *carbonic acid* that is eliminated by the skin is estimated at about 10 grammes in 24 hours, the results obtained by different observers varying, however, from 2·23 grammes to 32 grammes. The quantity increases with temperature and with muscular exertion. The quantity of *watery vapour* eliminated by insensible perspiration varies also with the temperature and moisture of the air, the amount of clothing and of exercise, and generally with all conditions that modify the flow of blood through the capillaries. It is difficult or impossible to separate and estimate it from sweat, but it is interesting to notice that it bears a certain inverse relation to the elimination of water from the system by the kidneys. When the temperature of the air is low, and when it is nearly saturated with watery vapour, the capillaries of the skin are contracted, little fluid is lost by cutaneous evaporation, and the kidneys secrete freely; while, on the other hand, if the air be warm and dry, the cutaneous capillaries are charged with blood, the kidneys secrete but a small quantity of water, and the insensible perspiration is greatly augmented.

The **cutaneous secretions.**—Regarded as an organ of *secretion* the skin presents a surface of about 15,000 square centimeters, or one and a half square meters, and secretes a fluid named sweat, and a peculiar sebaceous or oily material. *Sweat* is a colourless, slightly cloudy fluid, with a salt taste and characteristic odour; its specific gravity is 1004; its reaction is primarily alkaline, but from

its admixture with sebaceous matter which contains fatty acids, it, as ordinarily examined, gives an acid reaction. Its alkalinity can be shown in such regions as that of the palm of the hand, where there are no sebaceous glands. The quantity secreted per diem is about 1,000 grammes, or about 2 lbs.; but great variations result from differences of both internal and external conditions. Large quantities of fluid ingested, violent muscular exertion, high external temperature with dryness of the air, all tend to increase the amount of secretion, and if acting together may cause the elimination of many pounds of fluid per diem. Chemical analysis of the sweat shows that it contains about 1 per cent. of solids, of which urea, a proteid resembling casein, the neutral fats, palmitin and stearin, cholesterin, and the volatile fatty acids, are the most important organic constituents; whilst the inorganic include sodium and potassium chlorides, sulphates and phosphates.

Influence of the nerves on the secretion of sweat.—The nerves seem here, as in so many other cases, to influence the secretion in two ways; first, by influencing the size of the blood-vessels, and the activity of the circulation through the glands; and secondly, by a direct action on the gland-cells themselves. Paralysis of the constricting vaso-motor nerves, and stimulation of the dilating vaso-motor nerves, causes the blood to flow with increased rapidity through the blood-vessels of the glands, and the excretion of sweat is increased. This effect is well shown in cases where the sympathetic nerve in the neck has been divided, the skin of the face and neck on the same side as the lesion becoming moist with perspiration, whilst electrical stimulation of the upper cut extremity arrests the secretion. That a direct action can be exerted on the glands through the nervous system apart from any change in the circulation

is shown, first, by the fact that stimulation of the sciatic nerve will produce increased secretion of sweat, even in an amputated limb; and secondly, by the circumstance that if the sciatic nerve of one leg be divided, and the animal be placed in a hot temperature, and even if, in addition, the vein of the same leg be tied so that the conditions most favourable to congestion of the cutaneous capillaries are established, no secretion of sweat takes place from the damaged limb, though the others, with the rest of the body, perspire freely; but if, when the animal has cooled, a stimulus be applied to the peripheral extremity of the divided sciatic, a secretion of sweat immediately appears on the pads of the toes of the foot whilst none is excreted in the other limbs. If atropin, which checks the action of secretory nerves, be instilled before placing the animal in the warm chamber, no secretion appears. Hence it is not due to simple dilatation of blood-vessels.

The nerve centre for the secretion of sweat lies in the anterior part of the grey substance of the spinal cord, and the motor fibres partly issue with the motor roots of the nerves forming the sciatic nerve, and partly enter (in the cat) the sympathetic cord. The sweat centre can be stimulated *directly* (1) by venous blood; (2) by blood, the temperature of which has been artificially raised considerably above the normal; (3) by certain poisons, as by nicotin; and *reflectorially* by stimulation of the sensory nerves of the part. There must also be some fibres of communication between the brain and sweat centres, since the influence of mental conditions on the production of sweat is very marked.

The **sebaceous matter** secreted by the skin is the product of the cells of the sebaceous glands, situated near the roots of the hair, and opening into the hair follicles. It is at first fluid, but in process of

excretion forms a consistent mass that, as in the alæ of the nose in some persons, may be squeezed out in the form of a white wormlike body. Examined under the microscope, fat granules are found with the débris of cells, crystals of cholesterin, and, in many instances, a small acaroid animal, the Demodex folliculorum. Its chemical composition is olein with some soaps and cholesterin, the insoluble phosphates of lime and magnesia, and extractives. Its purpose is to lubricate the skin, diminish excessive evaporation, and render the hairs bright and glossy. The skin of the new-born child is sometimes covered with a layer of this sebaceous matter, which is then named the *vernix caseosa.*

The functions of the skin as an organ of sensation will be considered under the head of special senses.

CHAPTER XI.

ANIMAL HEAT.

The chemical processes which are constantly taking place in the living body consist essentially in the decomposition of complex organic compounds under the influence of oxygen, by which various forms of force are set free, and, amongst others, heat. Every living body generates heat, but in some the processes of oxydation are so slow and feeble that the temperature of the body does not materially differ from that of the surrounding medium, whilst in others they are so active that a tolerably constant temperature is maintained. The former class, represented by such animals as the fish and the reptile, are sometimes incorrectly named "cold-blooded," but more properly "poikilothermal" (ποικίλος, changeable); and the latter represented by the bird and mammal, improperly

"warm-blooded," but more appropriately "homoiothermal" (ὅμοιος, unchangeable).

Modes in which heat is lost.—There is a constant loss of heat from any body that is warmer than the atmosphere surrounding it, by three processes: conduction, convection, radiation; and, when the surface of the body is moist, by a fourth, named evaporation. In *conduction*, heat is lost, but to a small extent only, by the direct communication of heat from one particle of air to another. In *convection*, a considerable amount is lost by the establishment of currents of air, the particles of air that have been warmed by contact rising, and being replaced by colder layers. In *radiation*, heat is freely lost by the production of undulations or a conversion into motion which spreads in all directions from the heated body. Lastly, a very large quantity of heat is lost when *evaporation* occurs, owing to the conversion of specific into latent heat. Animal heat is generated to compensate for the loss of heat thus effected.

Calorimetry.—By calorimetry is understood the measurement of the total amount of heat produced in a given time by the body, and this is ascertained by placing the animal in a cage surrounded by ice or by water for a definite period, and collecting the water which proceeds from the melting ice or ascertaining the elevation of temperature which the water has undergone. In either case the amount of heat given off can by calculation be exactly determined. Instead of determining the amount of heat generated in this direct fashion, it may also be estimated by indirect methods, one of which is to calculate the quantity of carbon and hydrogen contained in a carefully analysed diet, and to compare it with that eliminated by the urine and fæces; the difference gives the quantity of these elements oxydised in the system. A second method is to ascertain the quantity of oxygen

taken into the œconomy, and the amount of CO_2 eliminated by the skin and lungs. The excess of oxygen not employed in oxydising carbon is supposed to be applied to the oxydation of hydrogen, sulphur, and phosphorus. In order that a reference may be obtained to which variations in the quantity of heat produced may be referred, it is found convenient to take as a unit of heat the quantity of heat required to raise one kilogramme of water at 0° C. one degree. This is called a *calory*, and the theory of the correlation of forces, supported by the experiments of Joule and others, has shown that there is a direct relation between heat and mechanical work. The unit of work which has been taken is named a kilogrammeter, and is that amount of force which is required to raise one kilogramme one metre high. It has been found by experiment that the expenditure of one calory is capable of raising 430 kilogrammes one metre high. That is to say, the mechanical equivalent of one calory is 430 kilogrammeters; and, *vice versa*, the friction or a blow caused by the vertical descent of 430 kilogrammes through one metre is equal to one calory. The mechanical work of the muscles estimated in kilogrammeters may be reckoned also in calories, since it is sufficient to convert calories into kilogrammeters to multiply them by the number 430, whilst to convert kilogrammeters into calories they must be divided by 430.

Mode of determining the temperature.—The instrument employed for this purpose is the thermometer, and as very minute differences have to be measured, it is expedient that the bulb should be large and the bore of the stem very fine. For convenience' sake, a small indicator is inserted into the bore in the form of a bubble of air separating a small segment of mercury from the main body, which shows the highest point reached, and obviates the erroneous

reading that would otherwise occur from the fall of the mercury during the interval between its contact with the body and the examination of its height on the scale by the observer in a good light. In England Fahrenheit's thermometer is in common use, in which zero is the point at which the mercury stands when ice and salt are mixed; and the space between which and that where the mercury stands when placed in boiling water is divided into 212 parts, the freezing point in water being at 32. On the Continent the thermometer of Celsius, or the centigrade thermometer, is used, in which the freezing point of water, or, rather, the melting point of ice, is taken as zero, and the boiling point of water as the upper limit, the space between these two being divided into 100. One degree centigrade is equal to nine-fifths of a degree of Fahrenheit's thermometer. To convert centigrade degrees, or the degrees of Celsius' thermometer, into those of Fahrenheit, multiply by 9, divide by 5, and add 32°. To convert those of Fahrenheit's scale into centigrade degrees, subtract 32, divide by 9, and multiply by 5. Thus, to convert 40°C. into Fahr. $40 \times 9 = 360$; $360 \div 5 = 72$; $72 + 32 = 104°$. Therefore, 40° C. = 104° Fahr. In order to determine the temperature of the body, or of any part of it, time must be given for the full expansion of the mercury, and this commonly requires two or three minutes. In man, the temperature of the body is usually ascertained by placing the bulb of the instrument in the axilla, and covering the stem with the bedclothes. In animals it is often taken by inserting the bulb into the rectum or vagina.

The temperature of different internal organs of the body has been determined, in some instances, by enclosing small thermometers, constructed to register maximum temperature, in a little metallic capsule, which the animal experimented on is made to swallow. They are re-obtained after having passed

through the whole length of the intestinal canal. In other instances, still more minute thermometers have been introduced into the vessels, and allowed to be carried for some distance.

Temperature of man.—It is remarkable that, notwithstanding the roughness of the instruments at his disposal, the estimate made by John Hunter (99° Fahr., or 37·2° C.) coincides with the most careful recent researches. Perhaps 100° Fahr. might be accepted for the general temperature of the interior of the body.

Circumstances modifying the temperature of the body.—*Influence of age.* The temperature of the child before birth is a little higher than that of the vagina of the mother, owing to independent production of heat and protection from loss. Shortly after birth the child cools rapidly. During childhood, and up to puberty, the temperature gradually falls about two-tenths of a degree centigrade. From puberty to the age of fifty it falls about two-tenths more. Charcot remarks that the temperature of the axilla in old people may be as much as 3° C. below that of the rectum. The temperature in old people is, however, nearly as high as in the new-born child, probably owing to anæmia of the skin, and consequent smaller loss by radiation; but, like infants, they have little power of resisting the depressing influence of cold. Sex has very little influence on the temperature.

Influence of the period of the day.—The results of many experiments show that the temperature of the body rises quickly from 6 a.m. to 10 or 11 a.m., and more slowly up to about 6 p.m., when it begins to fall, reaching its minimum between 4 and 6 a.m. The difference between the maximum and the minimum is about 1° C.

Influence of food.—As the oxydation of the ma-

terials which compose the food constitutes the source of heat, it is natural that the temperature should be modified both by their quantity and quality, and by the temperature at which they are introduced into the body, but the effects are slighter than might be expected. The temperature rises after food, but only a few tenths of a degree centigrade, and it is said even to decline if alcohol be taken. Hot fluids raise the temperature one or two-tenths of a degree, whilst after the ingestion of ice, or of a glass or two of iced water, the temperature may fall one or two degrees. The fall of temperature after the use of alcohol is to be explained by its effect in dilating the capillaries of the skin, thus allowing freer transpiration of watery vapour and radiation of heat, and this supplies a strong argument against the consumption of alcohol by those who are likely to be exposed to a very low atmospheric temperature. In inanition the oxydising processes continue in the body, which is, so to speak, living upon or burning itself, and the temperature remains unchanged until shortly before death, when it suddenly falls. When the decline amounts to about 23° or 24° C. death invariably occurs.

Influence of muscular exertion.—Muscles in contracting liberate heat, which is carried off by the blood circulating through them, and warms the body generally. The effect, however, soon passes away, owing to the existence of compensatory arrangements, such as more rapid respiration and more rapid circulation through the skin. A quick march of the duration of an hour and a half has been found to raise the temperature 1·2° C., whilst in tetanus, in which many muscles are thrown into a state of spasmodic contraction, the temperature has been seen to rise to 44·75° C. The same effects have been observed in dogs tetanised by the application of an electric current to the spinal cord; but it is to be noted that

there is not only increased liberation of heat in such cases owing to muscular contraction, but that the vaso-motor nerves may be stimulated, causing contraction of the cutaneous capillaries, and therefore diminished loss. Marcet found that when at rest during the ascent of Mont Blanc the temperature of the body did not vary much at different heights. Repeated vigorous contraction of a single muscle, like the biceps, causes its temperature to rise half a degree C., and the temperature of the body rises nearly half a degree C. during labour pains.

Influence of mental exertion.—A slight rise of temperature, varying from 0·5° to 1° C., occurs in the whole system as the result of intense mental effort.

Influence of surrounding temperatures.—Dr. Davy, who made many experiments in different climates on the temperature of man, found that climate had very little influence on the temperature of the adult white man. It scarcely differs more than 1° in the native of India and in the Icelander, though the absolute amount of heat generated in the two must differ to a very great extent. The larger quantity of heat which the man develops who lives in a temperature where the thermometer falls many degrees below zero, as compared with that generated by those who dwell in torrid zones, where the temperature does not, for a considerable part of the day, differ much from that of their own bodies, is derived, as we have seen, from the nature of the food, which is not only greatly increased in absolute quantity, but consists of compounds, like the fats, which in burning give off much heat. The degree of *moisture* in the air is of great importance, the influence of moist hot air being much more marked than of dry hot air, in consequence of the interference in the former case with the regulating action of evaporation from the skin. Many workmen are exposed without inconvenience to temperatures in

dry air, which would be quite unbearable were it even partially saturated with moisture, the ill effects of such exposure being prevented and the temperature of the body maintained at the normal standard by drinking freely of some watery fluid and by copious perspiration. Exposure to very high degrees of heat, especially if accompanied with exercise, is apt to cause death, either by apoplexy, as in the "sun-stroke" that occurs in summer even in temperate climates, or by "heat tetanus," in which the heart and respiratory muscles suddenly become rigid. A frog stiffens and dies if plunged into water at a temperature at, or a very little above, that of the blood of a mammal. The greatest cold which has been noted was by Capt. Back, who observed a temperature of −70° F., but, with sufficient food, little inconvenience is felt even by so low a temperature as this, providing the air is still. When the air is in motion, however, it is impossible to face it, and those parts of the body which are exposed, or remote from the heart, as the nose, ears, fingers, and toes, are certain to be frost-bitten or killed. The practice of rubbing such parts with snow to restore animation in them is right, as it prevents the vessels from yielding too suddenly to the influx of blood and becoming over distended. Exposure to cold under unfavourable circumstances, as under the influence of alcohol, may cause great reduction of the temperature of the body. Thus, in one case recorded, a drunken woman, after falling into a ditch covered with ice, remained in it all night. On admission into the hospital the temperature was found to be reduced to 26° C. In the course of six hours it had risen to 36·3° C., and she eventually recovered.

Cold may be applied externally and to limited region of the body for a considerable period, if the animal be otherwise well nourished. without materially reducing the temperature of the deeper lying

parts. Thus it has been found that immersion of the arm in man for an hour in iced water only lowered the temperature of the interior of the biceps, as determined by the thermo-electric needle, 0·2° C.

The sun the primary source of heat.—Terrestrial heat is derived from the sun, and the quantity the earth receives is inconceivable. It is calculated that with a vertical sun 3·4 calories per hour are received by each square foot of the surface of the earth, producing a heating effect equivalent to five billion cwts. of coal; or, reckoning the combustion of 7lbs. of coal per hour as equal to one horse-power, and taking into consideration that our steam-engines only utilise $\frac{1}{22}$nd of the absolute mechanical effects of heat, the sun's warmth is equal to 66 billion horse-power per hour. This is sufficient, as Tyndall points out, to melt, in the course of a year, a layer of ice 100 feet thick, over the whole surface of the earth, or to raise an ocean fifteen miles deep, of the same extent, from the melting point of ice to the boiling point of water; yet the earth only receives $\frac{1}{2\,200,000,000}$th of the total quantity of heat radiated by the sun.

Sources of heat in the body.—The generation of heat in the body proceeds chiefly from chemical, but in part from mechanical, processes. The chemical actions are the oxydation of the various substances ingested as food, which descend to lower and still lower planes of chemical composition, till at length they are eliminated from the body in the forms, already noticed, of water and carbonic acid, and of substances to be hereafter described, such as urea and uric acid, which are discharged by the kidneys; and it is important to remember that the quantity of heat generated by the combustion of these bodies is the same whether they are burnt directly with the free access of oxygen, or whether they pass through a succession of grades of more and more complete

oxydation. One grm. of hydrogen in combining with oxygen generates 34·462 calories, and one grm. of carbon 8·080 calories. One grm. of starch gives 3·2 calories, one grm. of albumin 4·998 calories, and one of fat 9·069 calories. The high heat-generating power of fat is due to the fact that it is entirely burnt up, whilst it contains originally very little oxygen. Starches and sugars have less power of generating heat, because the hydrogen they contain is already partly oxydised, whence their appellation of carbohydrates. And albumins, though they contain much carbon and hydrogen, are yet less effective than fats, because they already contain some oxygen in combination, and because they are not wholly consumed in the body, but are eliminated in the form of urea, one grm. of which is still capable, when burnt, of yielding more than two calories. Besides the processes of oxydation, the combinations of acids with bases, the absorption of water, as in the decomposition of fats, and the like, act in a subsidiary manner in the production of heat.

The **mechanical actions** generating heat are chiefly those of friction: such as the friction of the blood against the walls of the vessels, and of tendons in their sheaths; but inasmuch as the friction is the result of muscular contraction, which is attended with oxydation, even this may be regarded as principally due to chemical action.

The **locality of the generation of heat.**—Lavoisier maintained that as the lungs were the organs by which oxygen was absorbed, oxydising processes also took place in them, and that they might therefore be regarded as the foci or centres of heat in the œconomy; but were this the case, the lungs should be the hottest parts of the body, which experiment shows they are not. The chief centres of heat production are really the muscles, in which, even when

at rest, but especially when contracting, active processes of oxydation occur. A considerable quantity of heat is also disengaged in all glandular organs when discharging their functions, and the liver, the largest gland in the body, has been shown to develop so much heat, that the blood returning from it (that, namely, which is contained in the hepatic veins) possesses a higher temperature than that of any other part of the body. After the muscles and glands, the brain and nervous system are the principal organs which participate in the production of heat.

Total quantity of heat generated in the body.—If, with Ranke, the diet of a healthy man be reckoned on the following scale, it will be seen to what the total quantity of heat generated per diem amounts:

100	grammes of albumin	give	426·300	calories.
100	,, of fat	,,	906·900	,,
240	,, of starch	,,	938·880	,,
	Total . . .		2272·080	

In round numbers, a man generates per diem 2272 calories, which is equivalent to about one million kilogrammeters, *i.e.* would be capable, if converted into mechanical work, of raising one million kilogrammes one metre high. The force generated by the oxydation of the food is not altogether, though it is in part, expended in the performance of external mechanical work. Part is expended in warming the air and food introduced into the body, part is lost by radiation and conduction, and part is used up in the performance of internal work, as in the movement of the blood. The body may, therefore, be regarded in the light of an engine, in which the force liberated by combustion becomes apparent partly in the form of heat and partly in the form of work done.

Regulation of the temperature of the body.—As the temperature of the body remains

tolerably constant, while both the processes of oxydation and the external conditions which lead to loss of heat undergo considerable variation, it is evident that some regulatory influences must be in operation. The variations in the production of heat depend essentially on the amount of muscular exertion that is made, whilst the variations in the loss of heat depend partly on the state of the body and partly on the temperature of the surrounding medium, and the nervous system constitutes the necessary bond of union by which the conditions leading to the generation and the loss of heat are associated. The chief causes of loss of heat are: (1) The heat required to warm the air inspired. The average daily amount of air inspired, thirteen kilogrammes, which enters the body at a mean temperature of 12° C., and leaves it after being warmed up to 37° C., that is, after it has been heated 25 degrees, is estimated to require 84 calories. (2) The heat lost in heating the food and drink, amounting to 1900 grms., which is estimated at 47 calories. (3) The heat lost in cutaneous transpiration, which amounts to 660 grms., and requires 364 calories. (4) The heat lost by pulmonary evaporation, amounting to 330 grms., which requires 182 calories. These collectively account for 677 calories lost. The remaining 1595 calories, required to account for the 2272, are lost by radiation from the skin.

Expressing the modes by which heat is lost in the percentage form, Helmholtz considers that

2·6 per cent. of the total heat is expended in heating the food.
2·6 per cent. of the total heat is expended in heating the air inspired, supposing its temp. to be raised from 20° C. to 30° C.
14·7 per cent. of the total heat in evaporating the water eliminated by the lungs.
80·1 per cent. of the total by radiation, by conduction, and by evaporation of water from the skin.

The compensatory arrangements, by which the

temperature is maintained at a uniform standard, are : (1) In cases of increased generation of heat by promoting its loss. (2) In cases of diminished generation of heat, by preventing its loss. For example : If the external temperature to which the body is exposed be high, the arterioles of the skin relax, a freer current of blood passes through the capillaries, and radiation from the surface is increased, whilst at the same time evaporation of fluid, both by sensible and insensible transpiration, takes place, which powerfully contributes to lower the temperature. At high temperatures, moreover, the appetite for food is diminished, and there is consequently diminished production as well as increased loss of heat, so that on the whole the temperature of the body remains stationary.

Moreover, the respiratory acts are increased in frequency when the body is exposed to a high temperature. This condition, sometimes called heat dyspnœa, is probably occasioned by the direct action of heat on the nervous centres, and is clearly of a compensatory nature, the fresh supplies of air permitting the evaporation of more water from the blood, and thus tending to lower the temperature of the body.

If, on the other hand, the temperature of the surrounding medium be lowered, the arterioles and capillaries of the skin contract, and loss of heat by radiation is greatly reduced; food is taken in larger quantities, and of a nature like fat to yield more heat on oxydation, and the temperature is again maintained at an equable standard.

Value of clothing.—Animals that possess a high temperature preserve it when exposed to cold by a covering of hair or feathers, and even in man the unprotected skin is a very bad conductor of heat ; but, with the exception of parts of the tropical regions, some sort of covering is worn in all regions of the earth. In the warmer parts of the temperate zones,

cottons; in the cooler, single garments of silks and woollens; and in the cold regions, several coverings of the same materials, with, when the temperature is very low, the furs and skins of animals, as an outer investment, are employed. The bad conducting power of the atmosphere renders a series of these layers of clothing, including layers of air between them, more efficacious than one thick one. Mackintoshes and garments made of indiarubber are to be avoided, except for temporary protection against wet, since, being impermeable, they confine the perspiration, which speedily saturates the clothes with moisture.

Influence of the nervous system on the generation of heat.—The influence of the nervous system on the production of heat is rendered evident by the division of the sympathetic nerve in the neck. The effect of this is to relax the arterioles of the side of the head corresponding to the lesion, those of the ear, for example, becoming more conspicuous, and the temperature of that organ considerably increased, the difference between the two ears augmenting in proportion as the external temperature is low. Various circumstances tend to show that there is a generation of heat in those tissues, which thus receive a fuller and more abundant current of blood, and especially the fact that, if the head of the animal be enveloped in wool, the venous blood returning from the ear after section of the sympathetic may be actually warmer than the arterial blood passing to it, indicating that a local generation of heat takes place. The function of the sympathetic would therefore appear to be, when in the normal and uninjured state, to bridle the chemical changes, and consequently the development of heat in the tissues; it is not only, therefore, a vaso-constrictor nerve, but also a "frigorific nerve."

Stimulation of a sensory nerve, such for example as the *auricularis*, causes diminution of temperature

in the ear when the sympathetic is uninjured, but raises the temperature of the ear when the sympathetic is divided. In the first case a slight rise precedes the fall, which depends on reflex paralysis of the vaso-dilator nerves, and is not observed if the vaso-dilator nerves are stimulated by curare, because the action can then be exerted upon the vaso-constrictor nerves.

Division of the spinal cord is followed by a gradual fall of temperature till death occurs, the fall being more rapid in proportion as the cord has been divided at a higher point. If the section is made higher than the sixth cervical nerve, the respiratory nerves are divided, and artificial respiration must be maintained. The existence of a heat-regulating centre in the spinal cord is still debated.

Increased heat, either of a particular region or of the whole body, is a characteristic feature of inflammation, as may be seen in a boil on the one hand and in fever on the other. In the latter case the higher temperature is due to more rapid oxydation of the tissues taking place, and the force which should be used up in nutrition, growth, and in muscular action is misdirected, and expended in the production of heat. In this way the languor and debility which is associated with general fever may be in great measure accounted for. In the case of local inflammation the augmentation of heat in the part is mainly due to the dilatation of the blood-vessels and to the passage of warmer blood through them, and analogy renders it probable that it is in part due to increased oxydation, but the temperature does not rise above that of the interior of the body.

CHAPTER XII.

THE URINE.

Characters of the urine.—The urine is a fluid secreted continuously by the kidney, and is the chief means by which the nitrogenised waste products are discharged from the body. It is a clear amber-coloured fluid, with slight fluorescence, depositing a light cloud of mucus on standing. Its reaction is acid. Its mean specific gravity, 1020. Its odour is aromatic. It should contain no morphological elements except a few epithelial cells.

Quantity of the urine.—The average quantity of urine discharged by a healthy man per diem is about fifty ounces, or two pints and a half; but it varies greatly with the amount of fluid ingested, and with the evaporation of fluid by the skin and lungs. It increases with increase of blood pressure. It is greatest in the morning, less in the evening, and least at night during sleep. The first day after birth it is scarcely more than an ounce, but at the end of the first month it rises to half a pint or more, and from three to five years of age it is about a pint and a half; it is less in women than in men. It is increased by certain drugs, as potash nitrate and acetate, which are termed diuretics.

Specific gravity of the urine.—Though the average specific gravity is 1020 it exhibits great variations, the extremes being 1002, which occurs after drinking much water, and 1040 after abstinence from fluid, and copious perspiration. The specific gravity is essentially dependent on the quantity of solids relatively to that of the water. It is estimated

by an instrument termed a hydrometer, or urinometer which consists of a float weighted with mercury, and with a long graduated neck. The graduation begins *above* at 1000 because the heavier the urine the less deeply will the instrument sink, and the further the neck will protrude from the surface. If very little urine is accessible, the specific gravity may be ascertained by adding two, or three, or four times its volume of water, then taking the specific gravity with the urinometer, and multiplying the number obtained by two, three, or four, according to the number of volumes of distilled water that has been added. Attempts have been made to discover an easy method of estimating the quantity of solids in a given quantity of urine, and an approximation may be obtained by multiplying the two last numbers of the specific gravity by 2·2 or by 2·3. Thus, if urine be of specific gravity 1015; 15 multiplied by 2·2 gives 33. The number 33 represents the number of solid parts in 1000 of such urine.

Colour of the urine.—As a rule it may be said that the larger the quantity of urine, the paler it is; whilst the smaller the quantity, and the more concentrated it is, the higher the colour. The urine passed on rising in the morning is usually the most deeply coloured of the day. It is called *urina sanguinis.* That passed after copious draughts is pale, *urina potus.* The *urina cibi*, or urine passed soon after a meal, is intermediate in colour, and often cloudy. Some drugs, as senna, rhubarb, and especially the prickly pear, confer a deep colour on the urine. The colour of normal urine is due to urobilin, or to some modification of this substance, which is again derived from hæmoglobin, and is probably a product of the disintegration of the blood corpuscles.

The **reaction of the urine.**—The acid reaction of urine is due to the presence of acid phosphate of

sodium, and not to uric or other free acid. The acid sodium phosphate occurs in the urine in consequence of uric acid, hippuric acid, and CO_2 each seizing a portion of the sodium of the basic phosphate. The acid reaction is increased by fasting, muscular exercise, and the ingestion of acids, whilst it is diminished, and may become neutral or even alkaline, after food, apparently as the result of the separation of acid from the blood in the gastric juice leaving an excess of alkali. The ingestion of caustic alkalies and their carbonates, and of the salts of the vegetable acids, such as the tartrates, malates, and citrates, which become converted into carbonates in passing through the body, renders the urine less acid, neutral, or even alkaline.

The reaction of urine is ascertained by dipping into it a strip of violet litmus paper, which, when placed in acid urine, becomes red, and when in alkaline urine, blue. The *degree* of acidity is determined by finding how much solution of soda is requisite to make a definite quantity of urine exactly neutral.

Chemical reactions of the urine.—The addition of *hydrochloric acid* to urine renders it darker and causes the precipitation of uric acid crystals in the course of twenty-four hours. With great excess of hydrochloric acid urine becomes reddish-brown, violet, or blue. The addition of *sulphuric* or *nitric acid* deepens the colour of urine, and if the nitric acid be cautiously added, the surface of contact of the two fluids presents a reddish hue. The addition of *picric acid* causes crystals of uric acid to be precipitated. If acidulated with *nitric acid*, and immediately treated with *phospho-molybdic acid*, and made to boil, it assumes an indigo-blue tint. The addition of *alkaline* solutions makes urine cloudy from the precipitation of the phosphates of lime and magnesia. Urine causes the blue colour of iodine and

starch to disappear. A precipitate forms on the addition of barium chloride as well as with nitrate of silver, acetate of lead, and oxalate of ammonia; dilute solution of mercury nitrate renders it hazy, the cloud disappearing on agitation. Lastly, when heated with an ammoniacal solution of copper oxide it destroys its blue colour (Beaunis).

Chemical composition of the urine.—The urine contains on an average about 60 grammes (about 900 grains) of solids in twenty-four hours, of which 40 grammes (600 grains) are organic, and 20 grammes (300 grains) are inorganic.

The *organic* substances are partly *azotised*, partly *non-azotised*. The former includes urea; uric and hippuric acids; creatinin, xanthin, oxaluric acid; and sometimes allantoin. The latter includes oxalic and lactic acids, and glycose. Then there are certain compounds of sulphuric acid named phenol-sulphuric and cresol-sulphuric acid, and sulpho-pyrocatechuic acid, and certain colouring matters, as urobilin.

Lastly there are the inorganic substances, which include sodium and potassium chloride, acid sodium phosphate, phosphate of lime and magnesia, alkaline sulphates, and traces of ammonia and iron.

Many substances appear exceptionally in the urine either after the consumption of certain kinds of food, or in particular states of the constitution. Thus albumin may appear if a large quantity of white of egg be consumed. So also peptones are sometimes eliminated with the urine, and a diastatic ferment. In other instances mucin, inosite, hypoxanthin, leucin, tyrosin, and cystin are discharged. The appearance of albumin in large quantities, as shown by the formation of a dense precipitate on boiling, and the addition of nitric acid, is a well-known sign of a serious disease of the kidney, Bright's disease or albuminuria. The urine in this affection is uniformly

of low specific gravity, usually below 1010. The presence of sugar in the urine in considerable quantity is the characteristic feature of the disease known as diabetes, and the specific gravity of the urine in this affection is often high, sometimes remaining for a lengthened period at 1040.

The **organic constituents of the urine.**—(1) *Urea* $CO(NH_2)_2$. The biamide of CO_2, or carbamide. This is the most important constituent of urine, for in man it is the substance which contains by far the largest proportion of the waste nitrogen of the body; in fact, when the diet is such that the weight of the body is preserved the same from day to day, it may be accepted that almost the whole of the nitrogen which enters the body in the food is discharged from it in the form of urea. The healthy adult Englishman performing moderate work excretes about 500 grains of urea per diem, or about 1 oz. av., of which nearly one half by weight is nitrogen. The quantity is not materially different in the French and Germans, in whom it is given as varying from thirty to forty grammes, with an average of about thirty-four grammes (which is 524 grains), though their food differs somewhat in containing less meat. Women excrete less urea than men. Children, by reason of their activity, relatively more. In old age the quantity falls considerably. The quantity excreted may be expressed differently by stating that it is in the proportion of 0·5 grammes (7·5 grains) for every kilogramme (2 lb. 2 oz.) of body weight. Blood contains 0·025 parts per cent. of urea.

Physical and chemical characters of urea.—Urea is a crystalline substance, very soluble in water and in alcohol, but almost insoluble in ether. It dialyses with great rapidity. When quickly crystallised, the crystals are acicular, but, when slowly crystallised, they form four-sided prisms, with oblique

extremities, belonging to the rhombic system. They are without smell, but have a cool taste like that of nitre. Considerable interest is attached to urea, from the circumstance that it is capable of being formed artificially. Thus, it can be obtained from a solution of ammonium cyanate, with which it is isomeric, by evaporation. When heated to 120° C., it is decomposed into ammonia, which is volatile, and a residue of biuret and cyanuric acid. In putrefying urine, or when treated with strong mineral acids, or when boiled with the hydrates of the alkalies, urea takes up two equivalents of water, and becomes converted into ammonium carbonate, the reaction being represented by the formula $CO(NH_2)_2 + 2H_2O = CO(ONH_4)_2$. When acted upon by nitric acid, it breaks up into water, CO_2, and N.

The **separation of urea in a pure state.**—(1) Evaporate the urine of a dog, which has been well fed with meat, to a syrupy consistence; add alcohol; filter and evaporate the alcoholic extract; set aside to allow crystals to form.

(2) Evaporate human urine to one-sixth of its bulk; cool to freezing point; add nitric acid. Nitrate of urea falls, with colouring matter of urine. Separate the precipitate by filtration, dissolve in boiling water, and pass through animal charcoal. On cooling, crystals of urea nitrate form. Dissolve these in hot water, and add barium carbonate till effervescence ceases. The fluid now contains barium nitrate and pure urea. Evaporate it; exhaust with alcohol, and set aside to crystallise by slow evaporation.

Tests for urea in urine.—(1) Evaporate urine to half its bulk, and add strong HNO_3. Impure urea nitrate separates out.

(2) *Russell and West's test.*—This test consists essentially in decomposing urea into water, carbon dioxide, and nitrogen gas. The quantity of the

latter produced is a measure of the quantity of urea originally present. The method adopted to effect the decomposition is to dilute the urine to be examined, and to mingle it suddenly, by a special arrangement, with a solution of sodium hypobromite and caustic soda in a test-tube inverted over water. Decomposition immediately takes place according to the following formula: $CO(NH_2)_2 + 3NaBrO + 2NaHO = 3NaBr + 3H_2O + Na_2CO_3 + N_2$. That is, Urea + Sodium hypobromite + Caustic soda = Sodium bromide + Water + Sodium bicarbonate + Nitrogen. The nitrogen thus produced is given off as gas, and displaces the water in the graduated tube which is held over it. The gas is at first evolved briskly, but afterwards more slowly; to facilitate its evolution, the bulb of the tube may be slightly warmed with a spirit-lamp. After ten minutes, the amount of water displaced by the gas should be read off on the tube, which is divided into tenths. Each number on the tube represents one gramme of urea in 100 centimetres of urine. Normal urine should yield roughly 1·50 parts of nitrogen by this test. If urine contain albumin, it should be first heated with two or three drops of acetic acid and then filtered (Harris and Power).

(3) *Biuret test.*—Heat urea crystals cautiously in a dry test-tube till the smell of ammonia ceases to be perceptible; then add a few drops of solution of caustic potash and of copper sulphate, and a violet-red colour appears.

(4) *Liebig's test.*—The urine ought, in the first instance, to be deprived of the phosphates it contains; and for this purpose two volumes of urine are mixed with one volume of baryta solution, made by mixing two parts of a saturated solution of barium hydrate with one part of a saturated solution of barium nitrate. The precipitate which falls when the urine is mixed

with this solution is separated by filtration, and fifteen per cent. of the filtrate, which corresponds to 10 cubic centimetres of urine, are employed to be tested for urea by means of the mercurial test solution.

A mercurial test solution is prepared, one cubic centimetre of which will precipitate one centigram of urea. This is made by dissolving 96·855 gr. of mercuric chloride in water, precipitating with potash, washing the precipitate, dissolving it in a sufficient quantity of nitric acid, and diluting to one litre. This test liquid is tested with a two per cent. solution of urea. In applying it, it is poured from a graduated burette into the 10 cc. of urine, until the whole of the urea is precipitated in the form of $2(CON_2H_4)N_2O_5+4HgO$. The end of the reaction is recognised by taking a drop of the mixture from time to time, and adding it to a solution of sodium carbonate contained in a watch glass. A white precipitate occurs as long as the urea is in excess, but as soon as the mercuric nitrate is in excess, the precipitate becomes yellow, owing to the formation of a basic nitrate of mercury. Before concluding the operation the whole original mixture should be neutralised with mercuric nitrate, until the yellow colour appears. Then each cubic centimetre of the mercuric solution employed represents one centigram of urea.

Circumstances modifying the excretion of urea.—(1) *The nature and quantity of the diet.*—If the food contain much albumin, casein, glutin, or other proteid, the amount of urea is increased. If, on the other hand, the food contain but little nitrogen, the quantity of urea diminishes. A diet rich in proteids will cause the urea eliminated per diem to rise from about 35 grms. to 80 and even to 100 grms. in twenty-four hours, as is seen in some diabetic patients who eat an enormous quantity of food; whilst a farinaceous and vegetable diet makes it fall to 20

grms. Though in greatly diminished quantity, it still continues to be eliminated when food is wholly withdrawn; and, under these circumstances, there is a diurnal increase about mid-day and a diminution in the early hours of the morning. Parkes found, in a man placed upon a purely non-nitrogenous diet, that the daily excretion of urea fell on the second day from about thirty-three grammes, which he discharged on ordinary diet, to twelve grammes, and afterwards remained for some days with little change at seven grammes. Ranke, whose size and weight were considerable, found that after two days of fasting with either previous nitrogenous or non-nitrogenous diet, the quantity of urea fell to about seventeen grammes daily. The consumption of food at each meal is swiftly followed by a rise in the quantity of urea eliminated.

(2) *The influence of muscular exercise.*—The experiments that have been made both on animals and man show that muscular exertion causes a very slight increase in the amount of urea excreted. The experiments that are most relied on to establish this are those of Voit on the dog, those made by Flint and Parkes on Mr. Weston the pedestrian, and those by Parkes on soldiers. In Voit's experiments, a large dog, weighing about seventy pounds, was selected, and carefully trained, first, to perform certain regular work, as the turning of a tread-mill, the force required to accomplish which had been calculated with great nicety; and, secondly, to evacuate the contents of the bowels and bladder at stated intervals. The excreta of the dog, when under ordinary conditions and with his food and body weight in equilibrium, were then examined chemically, both in the fasting state and when consuming a minimum diet. It was then made to work, by turning the tread-mill for ten minutes at a time six times during the day, (1) when fasting except from water, and (2) when supplied with just

sufficient food to cover loss when no work was done. The results showed that there was an increase in the quantity of urea when work was done, but that the amount of increase was very small, viz. an increase of from 0·1 to 0·3 gramme in the fasting experiments when the total in repose was about one gramme per diem; and an increase of from 0·3 to 0·7 gramme in the experiments with food when the excretion of the animal at rest was about 7 grammes per diem. Voit drew the conclusion that, during work, the substance of the muscle cannot undergo any large amount of disintegration, as was generally supposed before his experiments were made, and that the force exerted must be derived from the oxydation of other materials, of which the fat of the body or of the food was the most probable.

The experiments of Fick and Wislicenus afforded important confirmation of the general truth of Voit's statement. These observers climbed an Alpine peak, the Faulhorn, the height of which is 1,956 metres, on food from which nitrogen was excluded. The work in the case of Fick, who weighed 66 kilogrammes, was 129,096 kilogrammeters, and in the case of Wislicenus, whose weight was 76 kilogrammes, 148,656 kilogrammeters. In addition, other muscular work was done within the body of each man, as the action of the heart and of the muscles of respiration, the exertion required to maintain the erect position and the movements of the arms, which would all add their quota to the products of muscular exertion. They took no albuminous food for seventeen hours previous to making the ascent, none during the ascent, which occupied eight hours, and none for six hours after; but they did take a moderate amount of non-azotised food, consisting of cakes made with rice, fat, and sugar, with beer, tea, and wine, as solid food. The urine of different periods of the experiment was care-

fully tested to determine the amount of urea. The periods selected were, that passed on the night before the ascent, that passed on gaining the summit, that passed after the descent, and, lastly, that passed after a full meal had been taken. The comparison of these specimens of urine showed that in both observers there was a slight *decrease* in the amount of urea in the urine during the ascent and after the descent, as compared with the period before the ascent, the quantity discharged by Fick in grammes per hour during the four periods indicated being 0·63, 0·41, 0·40, and 0·45, whilst, in Wislicenus, it was 0·61, 0·39, 0·40, and 0·51, the unanimity of the observations on the two men being remarkable. It would therefore appear that in man, as in the dog, muscular exertion causes but little perceptible disintegration or waste of the proper muscular tissue.

The chief element of possible error in this conclusion lies in the fact that it is assumed that muscular tissue, if wasted at all, would cause an immediate increase in the quantity of urea in the urine; but it is clearly possible that the decomposition of muscle into urea may not be immediate, and that other nitrogenous compounds may be formed, which may remain for some time in the body, and be only slowly eliminated from the body, and perhaps in some other form than urea. Gamgee, however, considers that Fick and Wislicenus' experiments show beyond all doubt that during and after muscular contraction the quantity of effete nitrogenous material which passes out of the body is by no means adequate to effect the mechanical work done in contraction. What they fail to show is, whether or not *any* nitrogenous waste occurs in muscle during activity. If the urea be taken as a measure of the decomposition of albumin or proteids in the body, it may be calculated that the quantity of proteids decomposed by Fick was 37·17 grammes, and

by Wislicenus 37 grammes. These numbers afford data for determining the exact amount of force generated in the oxydation of this quantity of proteids, and from Frankland's researches it is certain that the total burning of 37 grammes of albumin would only yield about 80,000 kilogrammeters of force; but we have already seen that Fick required upwards of 129,000, and Wislicenus of 148,000, kilogrammeters for the mere ascent, without reckoning the amount of force required for the operations carried on within the body. Experiments, similar to those of Fick and Wislicenus, were undertaken by Professor Haughton, who found that with a daily walk of five miles for five consecutive days the quantity of urea eliminated was 501·28 grains, whilst with a daily walk of 20 miles, other conditions remaining unchanged, the amount of urea discharged was 501·16 grains, or a trifle less than before. Prof. Parkes made a still more interesting series of researches on two soldiers at Netley. In one series the effects of work and of rest were contrasted in regard to the elimination of urea on a diet which was abundant in quantity but contained no nitrogen, and in a second series the effects of work and rest were contrasted on a normal diet containing nitrogen. In both sets of experiments it was found that there was a slight total increase of nitrogen eliminated during muscular exertion, though there was, as in Haughton's and in Fick's experiments, at first, and for about 36 hours, a slight *decrease* in the amount of nitrogen eliminated when work was performed. The decrease was subsequently over-compensated by an increased discharge of urea. In the experiments on Weston, who, in one instance, walked 100 miles in 21 hours 39 minutes, and subsequently attempted, but failed, to walk 400 miles in five consecutive days, were important, because Dr. Flint determined on the last occasion the elimination of nitrogen by the

urine for five days before the walk and for five days after it. Mr. Weston was 31, weighed 126 lbs., smoked moderately, and was an almost total abstainer from alcohol. A sample of every kind of food consumed was carefully analysed. During the five days of the walk Weston consumed in all 1173·8 grains of nitrogen in his food, and he eliminated 1807 grains of nitrogen in the urine and fæces. This leaves 633·8 grains of nitrogen over and above the nitrogen of the food, which it seems probable must be attributed to the waste of the tissues, and probably almost exclusively to the waste of muscular tissue. In this experiment Mr. Weston broke down on the morning of the fourth day clearly from utter exhaustion of the nervo-muscular apparatus, and it is probable that this was the result of insufficient sleep and food. It is enough to add that in Pavy's experiments on Weston, though he lost weight, the nitrogenous waste during the walking period was incompetent to account for the mechanical work done.

The results of all these experiments, then, seem to demonstrate that there is a slight increase in the total excretion of nitrogen after exercise, and this probably in part proceeds from the disintegration of muscular tissue. But the relation of waste of the proper tissue of muscle to the amount of work done may not inaptly be compared with the loss undergone by the iron framework of a locomotive whilst running. During action a part of the framework is disintegrated and cast off, but the wear and tear of the machine is comparatively trifling; the real source of the power is the fuel in the one instance and the carbohydrates and hydrocarbons supplied by the food in the other

Origin of urea.—Urea, with carbonic acid and water, must be regarded as the final stages of the regressive changes through which the albuminous compounds pass in their transit through the body.

Some, but not all, of the steps by which the proteids are converted into urea are known. In the alimentary canal, for example, they are first converted by the action of the gastric juice into peptones, and these again, by the action of the pancreatic ferment, yield leucin, glycin, tyrosin, and asparaginic acid, whilst, by putrefaction, the proteids yield various salts of ammonia. Similar changes take place in the proteids in the organs and tissues of the body after their absorption in the blood, and a number of compounds have been isolated, such as allantoin, alloxan, xanthin, hypoxanthin, guanin, and uric acid, which are so closely allied to urea that some, especially the last two, replace it in the urine of various animals, or appear instead of urea as the result of some disturbance of the œconomy, whilst the relationship is further shown by the circumstance that if administered with the food they greatly augment the quantity of urea excreted. The best physiological chemists admit, however, that it is not at present possible to arrange a table in which the albuminous compounds shall appear at the head of the list and urea at the bottom. An approximation may be made, no doubt; but there must be many gaps, and it seems probable that the immediate antecedents of urea are either carbonic acid and ammonia which unite with subtraction of water; or carbaminate of ammonia; or, lastly, cyanate of ammonia.

Is urea, then, a substance formed from the blood by the cells lining the tubules of the kidney, just as the cells of the mammary gland are believed to form milk; or does it pre-exist in the blood, and, being formed elsewhere, do the renal cells merely act as filters, and free the system from urea, just as sodium, chloride, potassium, phosphate, or any other salt, is eliminated? There can be no doubt that the blood contains urea in all parts of the system, though the quantity is

extremely minute. In arterial blood it is present in the proportion of about 1 part in 10,000, but in the blood that has just traversed the kidney the proportion sinks to about 1 part in 20,000. The minute quantity that exists at any moment does not, however, form any bar to the elimination of large quantities in a given time if we admit that the flow of blood through the kidneys is very large, and that the renal cells seize upon it with avidity, and remove it as fast as it is formed. That these cells are not essential to its production is rendered evident by the results of extirpating the kidneys, or of applying a ligature to the renal arteries, or to the renal veins, for in all instances urea begins to accumulate in the blood, and may, in the course of twenty-four hours, increase from two to eight times its former proportion. The accumulation of urea in the blood as the result of pathological conditions, in which microscopical examination shows that the function of the kidneys is abolished, is well known, and in such cases urea is sometimes discharged with the sweat in such quantities as to form a crystalline deposit on the surface of the skin. When, however, we ask where, and in what organ, urea is formed, the question can only be doubtfully answered. The composition of urea points to its origin from the proteid constituents of the body, and the uniformity with which it is excreted, even during fasting, shows that it must be always in course of production; but it is remarkable that none is contained in the muscles, and little, if any, in the brain and nervous system, which together form so large a part of the body. It is, however, constantly present in the liver, and has sometimes also been found in the spleen and lymphatic glands, and these organs are known to be the seat of very active chemical changes. It has been, therefore, very generally held, that a part at least of urea is here formed; and this view is

supported by the fact that, in disease of the liver, attended with fatty degeneration of its cells, material diminution in the excretion of urea occurs. But it is conceivable that the muscles and nerves may, as a stage in their disintegration, generate compounds which may be convertible into urea, and in this point of view great interest attaches to those bodies which are so closely allied to urea, and which can be extracted from muscle. Examples are found in kreatin, which, when boiled with baryta water, breaks up into urea and sarkosin; in leucin, which, when ingested with food, rapidly reappears as urea in the urine; and in glycin, tyrosin, xanthin, sarkin, and the like, which have a composition more or less resembling urea, and are obtained from many different organs and tissues.

Several observers have, however, noticed that the quantity of urea in the blood after ligature of the ureters is much greater than after ablation of the kidneys, which supports the view that the kidneys themselves aid in its production; and if this be admitted it is probable that it proceeds from the metamorphosis of kreatin, the quantity of which is always increased in the muscles after the ureters have been tied. An increase of urea quickly follows the digestion of proteids. Yet it is remarkable that when peptones are directly introduced into the blood by intravenous injection, upwards of 80 per cent. reappears in the urine unchanged. A view recently advanced is, that urea does not proceed from a process of disintegration, but rather from a kind of synthesis taking place in the blood and tissues of the non-nitrogenous and nitrogenous terminal products of the proteids, that is to say, from a combination of carbonic dioxide and ammonia (Drechsel).

Uric acid $C_5H_4N_4O_3$.—This compound is closely allied to urea, and is the chief mode in which nitrogen is eliminated from the body by birds, reptiles,

and insects. The ordinary quantity that is discharged in a healthy adult per diem is about 0·75 gramme, or 10 grains, the proportion to urea being about 1 : 50; but if the diet be highly nitrogenous it may rise to 2 grammes or more. Uric acid is colourless, without taste or smell, crystallises in various forms, the type of which is the rhombic tablet. It does not exist in the free state in the urine, but forms an acid urate of sodium and potassium. It is very insoluble in water, one part only being dissolved in 18,000 of cold and in 15,000 of hot water. Hence when formed in excess it is apt to appear as a red sediment in the urine, to accumulate in the pelvis of the kidneys, forming a singularly painful form of stone, and to be deposited, in combination with bases, in the joints. Uric acid is a less perfectly oxydised compound of nitrogen than urea, and therefore makes its appearance when with abundant food there is insufficient respiratory activity.

Tests for uric acid.—1. The addition of a few drops of hydrochloric acid to urine causes uric acid to separate in the course of a few hours in the form of crystals, the form of which may be recognised under the microscope.

2. *The murexide test.* — Uric acid or urates when gently heated in a saucer with nitric acid become yellow and decompose into N and CO_2, which are volatile, and urea and alloxan, which remain. If these are slowly evaporated to dryness, and a drop of ammonia liquor being added murexide or ammonium purpurate forms with the production of a purple-red tint, which is very characteristic.

3. *Silver test.*—Drop a drop of the fluid containing a urate or uric acid dissolved in an alkaline carbonate upon a piece of blotting paper saturated with solution of silver nitrate, and a black spot appears, owing to reduced silver.

Quantitative determination of uric acid (*Salkowski's method*).—Take 200 centimetres of urine, and make strongly alkaline with sodium carbonate. In the course of an hour add 20 centimetres of concentrated solution of ammonium chloride, which causes a precipitate of acid ammonium-urate. The mixture is set aside for 48 hours in a cool place, passed through a weighed filter, and washed. Sufficient dilute hydrochloric acid is poured on the filter to dissolve all the ammonium urate, the filtrate being received in a clean glass. After six hours' standing, the whole of the uric acid separates, and is collected and placed on the same filter. The filter is twice washed with water and with alcohol till the acid reaction disappears. It is then dried at 110° C. and weighed. To the weight must be added, in addition to the weight of the original filter, 0·030 gramme.

The **place of origin of uric acid.**—Experiments to determine this point have been made on birds and on snakes, and it has been found that a few hours after the ligature of the ureters in birds, the canaliculi of the kidneys are filled with urates (which, however, are not found in the Malpighian capsules), and that at a subsequent period a deposit of urates takes place on the surface of all the serous membranes, the lymphatics of which are completely occluded by amorphous precipitate of these salts; it also appears on the joint ends of bones, in the parenchyma of the lungs, and elsewhere, whilst the blood, which under normal conditions is free from uric acid, contains a quantity large in proportion to the time that has elapsed after the performance of the operation. Parallel experiments in snakes are followed by the same effects; but if in these reptiles the kidneys are extirpated, very little deposit of the urates occurs, and none is found in the muscles, lungs, or liver. The conclusion is therefore obvious,

that uric acid is chiefly formed at the kidneys, and by the action of the cells of those organs.

Kreatinin $C_4H_7N_3O$.—This substance proceeds from the kreatin contained in muscle, from which it may be obtained by heating it in water, when H_2O is given off. From 0·5 to 1·5 grammes are eliminated per diem by an adult. It does not appear to be contained in the urine of the infant at the breast. It is a strong base, crystallising in colourless oblique rhombic prisms. It is increased on an albuminous diet, and diminishes materially when no food is ingested. When boiled with baryta water it breaks up into urea and sarkosin.

Hippuric acid $C_9H_9NO_3$ is found in small quantity in the urine, about one gramme being eliminated per diem, especially after the use of certain articles of diet, as after asparagus, greengages, and the ingestion of benzoic, kinic, and cinnamic acids. It is largely contained in the urine of herbivora, and in them proceeds from the cuticular tissue of plants, which is nearly allied to it in composition.

Xanthin $C_5H_4N_4O_2$ is an amorphous yellowish-white powder, which dissolves with tolerable facility in boiling water. Traces of it are found in the nervo-muscular system, and in some glands. It exists in urine in the proportion of about one gramme in 300 kilos of urine. It is intermediate in composition between sarkin and urea. Heated with a drop of nitric acid it yields a yellow stain, which becomes yellowish-red with potash, and on further heating violet-red.

Hypoxanthin or **Sarkin** $C_5H_4N_4O$. — This substance has only been found in the urine in leucæmia, but has been obtained from muscles and various glands. It is of interest on account of its near relationship to urea and to xanthin. From the former it can be obtained by the action of hydrogen

upon it in the nascent state, and it can be converted into the latter.

Oxaluric acid $C_3H_4N_2O_4$.—This substance is found only in small quantity in the urine in the form of ammonium oxalurate.

Allantoin $C_4H_6N_4O_3$.—Allantoin is found in the urine of the new-born child for the first few days after birth. It is especially interesting from its relation to uric acid. For it can be shown that uric acid under the influence of oxydising agents yields alloxan and urea. Alloxan by oxydation yields CO_2 and parabanic acid. Parabanic acid + H_2O gives rise to oxaluric acid, and oxaluric acid when dissolved in water and heated yields oxalic acid and urea.

II. Nonazotised Constituents of the Urine.

Oxalic acid $C_2H_2O_4$.—Oxalic acid, which has just been shown to proceed from the decomposition of oxaluric acid, exists in small quantity in the urine in the form of oxalate of lime; it is augmented by the use of all foods containing oxalates, as tomatoes and rhubarb, and by fruits containing citric acid.

Lactic acid $C_3H_6O_3$.—This acid is found in the urine after violent muscular exertion, and is probably always present in minute proportion.

Sugar.—The quantity of sugar in normal urine is, if any, very small, though in conditions of disease it increases to a remarkable extent. It is sometimes, in abnormal conditions, replaced by *inosite*.

Succinic acid $C_4H_6O_4$ is found after meat diet, and especially after eating asparagus and after the ingestion of alcohol.

III. Conjugated Sulphur Acids of the Urine.

Indican.—This substance, sometimes named *indigogen*, results from the combination of SO_3H with

indol. It is a brownish-yellow, bitter, disagreeably-tasting, syrupy substance, which is a stronger acid than acetic or hippuric acid. It exists in small proportions only in the urine. Its quantity is increased by any circumstance that delays the passage of nitrogenous aliment through the intestine, as by ligature of the intestine. It is augmented after the ingestion of indol. Its presence in the urine may be demonstrated by adding to a drachm of urine some strong hydrochloric acid with a drop or two of nitric acid. On heating, a violet-red colour appears, with the separation of rhombic crystals of indigo-blue and indigo-red. The same change is induced by putrefactive changes, and a coloured pellicle consisting of microscopic crystals of indigo-blue may not unfrequently be seen on the surface of decomposing urine.

Phenol C_6H_6O, or *carbolic acid*, exists in the urine in combination with sulphuric acid, as phenol-sulphuric acid, $C_6H_5O + SO_3H$, which forms salts with the alkalies. The pheno-sulphates form about one-tenth of the sulphates eliminated by the kidneys. The quantity of phenol is increased by the ingestion of phenol, tyrosin, benzol, and indol. The acid named *creso-sulphuric*, and the *sulpho-pyrocatechuic* acids, are occasionally present.

IV. Colouring Matters of the Urine.

Urobilin.—This substance is a product of the metamorphosis of hæmatin, and is associated with the colouring matter of the bile. It confers upon the urine its red or reddish-yellow colour. It is especially abundant in the urine of febrile patients. Another substance, termed *urochrome* has also been recognised, which oxydises when exposed to the air, and yields uroerythrine, which colours the precipitates of sodium urate.

V. Salts of the Urine.

The more important salts contained in the urine are:

1. **Sodium chloride,** of which about 11 or 12 grms. are excreted per diem, or 0·176 grm. per kilo of body weight. Women excrete less, and children still less. There are two periods of the day at which maximum quantities are eliminated, one in the morning and the other in the afternoon. It diminishes to two or three grammes in inanition. It is increased by the ingestion of food, and by muscular and nervous work.

2. **Phosphates.**—The quantity of phosphoric acid daily discharged is, on the average, 2·8 grms., or 0·044 grm. per kilo of body weight. One-third of this is combined with lime and magnesia, the other two-thirds with the alkalies sodium and potassium. The acid sodium phosphate gives its acid reaction to the urine. The quantity of the phosphates eliminated is augmented by abundant food, by muscular work, and by the ingestion of phosphates. They are increased by mental work. The elimination of phosphates is, for obvious reasons, less free during pregnancy, and during the early years of growth and development.

3. **Sulphates.**—A man eliminates about two grammes of sulphuric acid per diem, or 0·032 gramme per kilo of body weight. It is combined with sodium potassium and ammonium. The quantity is increased by food and by muscular exertion.

4. **Ammonia.**—The quantitity of ammonia eliminated by the urine in twenty-four hours is about 0·7 gramme. It is increased by some articles of diet, as asparagus.

5. The carbonates and bicarbonates of Na, Ca, Mg, and NH_4O are commonly present.

Spontaneous changes in urine on standing.—Urine, on standing in a cool place, first becomes more acid, owing to the development of an organic ferment (fungus), which acts on the minute quantity

of sugar contained in the urine, and leads to the development of lactic and acetic acids, the presence of which causes the precipitation of uric acid, acid sodium urate, and lime oxalate, rendering the urine cloudy. After the lapse of some time the urine passes into alkaline or ammoniacal fermentation, a bacilliform *micrococcus urinæ* appearing, which decomposes urea with addition of water into ammonium carbonate. Urea $CO(NH_2)_2 + 2H_2O$ = ammonium carbonate $CO_3(NH_4)_2$.

Mode of secretion of the urine.—The conditions under which the urine is secreted differ from those of all other glands in the circumstance that the capillary vessels constituting the tufts of Malpighi enter, without the intervention of any lymph spaces, directly into relation with the gland tissue, separated from it only by a delicate layer of epithelium and the capillary wall. In other parts of the gland, however, the usual arrangements prevail. Mr. Bowman pointed out long ago that the disposition of the blood-vessels in the Malpighian capsule was eminently favourable to the transudation of the watery parts of the urine, and that it was probable the salts were also excreted at this point, whilst the essential constituents of the urine, as the urea, were eliminated by the cells lining the convoluted portion of the tube, and were washed away by the fluid coming down from the capsule. In the Malpighian body a small artery breaks up suddenly into a tuft of capillaries covered with squamous epithelium, and there can be no doubt that under ordinary circumstances the pressure of the blood in these capillaries must be relatively high, and that the conditions are favourable to the filtration of water into the renal tubules. The efferent vessel from the Malpighian tuft again breaks up into a network of capillaries, distributed over the convoluted portion of the tubules. The pressure of the blood in this extensive secondary

plexus must be much less than in the capillaries of the Malpighian tufts; the current must be retarded, and time therefore afforded for the cells to abstract from the blood the more important constituents of the urine. By Ludwig, on the other hand, and his school, the urine is believed to be secreted in a dilute condition, with all its constituents, in the Malpighian tufts, with a rapidity varying with the blood pressure. As it descends the tubes it becomes more or less concentrated, in accordance with the laws of diffusion and the density of the fluids moving in the spaces surrounding the convoluted portion of the tubes. The result of recent enquiries, and especially those made by Heidenhain, on the whole favour the view taken by Bowman, for he has shown that certain substances are excreted by the cells of the convoluted portion of the tubes, and not by those of the glomeruli, and hence that the functions of these two sets of cells are different. Thus, if a few minims of a solution of a pure sulpho-indigotate of soda be injected into the blood of a rabbit, after section of the cord, which is done to reduce the blood pressure, and to allow a slower current of blood to traverse the kidneys, it will be found that if the animal be killed, the cells of the convoluted portion of the kidney will, in the course of a few minutes, be stained of a blue colour, whilst those lining the capsules are quite uncoloured. If, however, an hour be allowed to elapse, neither set of cells presents any coloration, but the granules of colouring matter lie free in the lumen of the tube, none being contained in the capsules, clearly showing that the cells lining the convoluted tubes have seized on the sulpho-indigotate of soda, and have excreted it into that part of the tube to which they are attached. When a part of the renal surface is destroyed by the application of nitrate of silver, the colouring matter, instead of being washed away by the water discharged

by the glomeruli, remains *in situ*. Whether the excretion of the urea and salts and of the water are simultaneous processes, or whether the solid constituents are first excreted into the lumen of the tubes, and are then swept away by a flush of water from the glomeruli, is unknown. In the frog, the watery excretion of the glomeruli is effected at the expense of the blood of the renal artery, whilst the convoluted tubules receive their vessels from the renal portal system. The secretion of urine is at once arrested if a ligature be placed upon the renal artery.

Influence of blood pressure on the secretion of urine.—The kidneys receive a very large proportion of blood, and in dogs it has been found by experiment that the arteries can be compressed till they are not more than about half a millimetre in diameter before the flow of blood through the veins is sensibly diminished, thus showing that the quantity of blood reaching the veins is, within wide limits, independent of the calibre of the arteries, but depends essentially upon the blood pressure, and the resistance it meets with in the organ itself. When the blood pressure in the aorta falls below 40 to 50 mm. Hg. the excretion of water by the kidneys is entirely arrested; but above this pressure the amount of watery excretion is directly dependent on the variations of the blood pressure. The quantity of urine discharged diminishes, therefore, on stimulation of the vagus, after hæmorrhage, and after section of the cord. On the contrary, it is increased by those conditions which cause either general increase of blood pressure or local increase of the pressure of the blood in the renal arteries. Thus, if a ligature be applied to the aorta below the origin of the renal arteries, or if several of the larger arteries of the body be tied so that the pressure of the blood in those that remain patent is exalted, or if cold be applied to the skin,

a larger quantity of blood flows under greater pressure through the renal vessels, and the quantity of urine discharged is much increased.

Local variations of blood pressure produce the same effects as general variations. Thus the local pressure of the blood in the kidneys can be increased by section of the renal vascular nerves proceeding from the splanchnics, and by puncturing the medulla oblongata, and in both cases, though the blood pressure generally is not affected, a great increase in the flow of urine occurs. But if the renal arterioles are made to contract by electric stimulation of the splanchnic nerves or of the spinal cord, the local pressure in the capillaries of the kidneys diminishes, and the quantity of urine falls. Ligature of the renal arteries arrests the secretion of urine.

Ligature of the renal veins, though it greatly increases the pressure in the capillaries, causes diminution of the flow of urine, which is evidently due to the great reduction it occasions in the quantity of the blood traversing the kidneys, and also, perhaps, to its interference with the nutrition of the secreting cells.

The quantity of the organic constituents does not depend on the pressure, as is clearly shown by the increased quantity of urea eliminated, when, other conditions remaining the same, the quantity of urea in the blood is increased by injecting it into the veins; and this occurs even where the blood pressure is greatly lowered by section of the spinal cord. The elimination of their constituents cannot therefore be by any means regarded as a mere process of filtration. The disposition of the vessels of the kidney, and the peculiar and varying characters of the epithelium lining the different parts of the tubules, are very suggestive.

There seems to be a certain alternation in the activity of the two kidneys, so that when one is

secreting vigorously the other is relatively quiescent. Variations in the composition of the blood materially modify the activity of the kidneys.

Pressure under which the urine is discharged.—If a mercurial manometer be inserted into the ureter of an animal, it is found that the pressure under which the urine is secreted will rise until it supports a column of mercury 60 mm. in height, when secretion stops. The pressure of the blood in the aorta in the same animal was observed to be from 100 to 105 mm. of mercury.

Micturition.—The urine as it is secreted collects in the bladder and is discharged at irregular intervals, but usually four or five times a day. The bladder holds about one and a half pints, and the pressure of urine in it in the healthy man produces no effect till it has accumulated to a moderate amount, when some discomfort is felt, and, by a slight effort of the will, the bladder contracts and completely empties itself. If this amount be much exceeded the desire to evacuate it becomes imperious, and if it cannot be gratified pain is experienced, and violent straining efforts are made. The nervous mechanism appears to be that there is a "micturition centre" in the lumbar region of the spinal cord, to which sensory fibres convey impressions from the mucous membrane of the bladder, and from which motor impulses are transmitted to the bladder. This centre is under the control of the will. Under ordinary circumstances, the stimulus of the bladder, when moderately full, is conducted to the centre, and the requisite motor impulse is transmitted to the detrusor urinæ, and the urine would be discharged were it not that the sphincter vesicæ is contracted, and requires a relaxing impulse to be liberated. This impulse *may* proceed from the cord, but probably ordinarily emanates from the brain, in order that a convenient time and place may be

selected; and the experiments of Ott seem to show that the inhibitory centre for the vesico-spinal centre is situated near the upper end of the crura cerebri. As soon as the sphincter is relaxed the detrusor acts and the urine is discharged. That the act is in part voluntary is within the experience of every one; but that the whole nervous mechanism, including reflex contraction of the detrusor muscles, and the relaxation of the sphincter, is under the control of the centre in the lumbar region of the cord, is shown by an experiment of Goltz, in which, the cord of a dog being divided in the dorsal region, the application of a sponge dipped in cold water to the perineum at stated intervals, led ultimately to the discharge of the urine at these periods, though under ordinary circumstances division of the spinal cord leads to retention and then to incontinence, the urine dribbling away as fast as it is formed, owing to loss of tone of the sphincter muscle.

CHAPTER XIII.

MUSCULAR MOVEMENT.

The movements that are observed in the body are referable to one of three kinds, *amœboid* movement, *ciliary* movement, *muscular* movement.

Amœboid movement. — The amœba is an organism presenting great simplicity of structure, if structure it can be called, when it appears only as a minute speck of animal jelly or protoplasm. When unexcited by mechanical or other stimulus, it forms a disk with irregular outline, in which slow movements can, by careful observation, be seen. These consist in protrusions of one part of the mass or another, which

often extend to a considerable distance from the main body, and, after acting as feelers, are either again retracted, or draw after them the rest of the body. The movements of the amœba are most active at and about a temperature of 36° C., but they cease or become imperceptible towards the freezing point, and when the temperature is raised as high as forty-five degrees. The irritability or contractility of protoplasm is rendered evident by the application of a stimulus whilst it is performing these slow movements. The mass then draws itself together and assumes a spheroidal form. The stimulus may be mechanical, as by the contact of a needle; chemical, as by the addition of some salt; thermic, or electric, or even the simple change from light to darkness or from darkness to light. In all cases it must be of a certain degree of intensity, and must be sudden in its application.

Ciliary movement.—The cells of many parts of the body present processes of their protoplasm, which, during life, and for some time after death, execute rapid vibratory or lashing movements, the effect of which is to drive the fluid in which they move, with any particles that may be suspended in it, towards the outlet of the body. The movement does not appear to be under the influence of the nervous system, but it is affected by external agents, moderate heat accelerating, cold retarding it. The extent of motion of the individual hairs is through an arc of fifty or sixty degrees, or occasionally as much as ninety degrees, and they are usually set in an inclined position in regard to the cell, bending forwards. The forward stroke of the hair is more rapid than the return stroke, and, when moving slowly, the movement runs in the form of a wave along the hair like the undulation of the lash of a whip. In some instances the motion resembles that of the arm in circumduction. The rapidity with which the strokes succeed each other is very great,

for even when considerably retarded by chemical agents or loss of power, they still may be as many as six or eight in the second. Attempts have been made to estimate the force of ciliary movement, and it appears to be much greater than that of striated muscle. The weight that can be distinctly moved, when covering a surface of one centimetre, by ciliary motion is accepted as its absolute force, and it has been found that the lowest value for the pharyngeal mucous membrane of the frog was 3·36 grammes. Ciliary movement may be observed to occur between 0° C. and 45° C., and the most rapid motion is observed when the cells are exposed to temperatures near the higher limit. If heated beyond this the motion begins to fail, and ultimately leaves the cilia all inclining forwards. Restoration of motion may occur on cooling, but at temperature of about 48° C. the motion ceases altogether and permanently. Short exposure to the temperature of melting ice temporarily suspends movement, which may, however, recommence when the temperature rises, provided the cilia have not been quite frozen. The presence of water is requisite for ciliary movement, and also of oxygen, the motion soon ceasing when oxygen is wholly withdrawn. Exposure to oxygen under a pressure of eight atmospheres or more arrests the motion. Ozone always acts as a poison. Alkalies and acids alike prove fatal to the movement of cilia, even in small doses. Small doses of ether, alcohol, amyl nitrite, and carbon bisulphide first accelerate, and then in somewhat large doses stop the motion. Chloroform arrests it without a primary stage of acceleration. The ordinary vegetable poisons, veratria, strychnia, atropin, eserin, curare, quinine, morphia, and hydrocyanic acid, do not appear to be more injurious than various indifferent substances, according to the degree of concentration.

Moderately strong currents of electricity act as

excitants, strong currents or shocks kill the cells and stop the movement. On theoretical grounds it has been supposed that there must be in the substance, or forming the substance of the cilia, serially arranged particles, which, when at rest, are elongated, and when in action are contracted, and the movement of which takes place in response to external stimuli, which here act directly and not through the intervention of a nervous system.

The object of the motion in many of the lower animals is to sweep aliment into the mouth, and to maintain respiration; but in man it is limited, in general, to the propulsion of mucus and any particles of matter, as dust, the débris of cells, and in some instances the products of secretion, towards the external orifice of the cavity or tube lined by the ciliated cells.

Muscular tissue.—The muscles, which constitute forty-five per cent. of the weight of the body, are the agents by which the movements of the body and its members are effected. There are two varieties, the striated and the unstriated, the former of which are usually, though not always, under the control of the will, the heart being a notable exception. (For the details of structure, *see* companion volume, Klein's "Histology.") The striated muscles consist of *fasciculi*, bound together into a mass by *perimysium*. The fasciculi can be split into fibres having a length of about one and a half inches in the longest specimens, though only a fraction of this in many of the more minute muscles, and a tolerably uniform diameter of about $\frac{1}{400}$th of an inch. The *fibres*, between which are the blood-vessels and nerves, are composed of a transparent nucleated sheath or *sarcolemma* enclosing fibrillæ. The fibres may be split either transversely or longitudinally; in the former case each fibre seems to be composed of a

series of disks, in the latter of a series of fibrils. If a *fibril* be examined it is seen to present alternately disposed dark and light portions, and these being arranged on the same plane in adjoining fibrils, confer upon the fibre which they form its striated aspect. The dark particles are anisotropous, or doubly refracting. The isotropous, or bright and clear bands, are singly refracting. The substance of the fibrils is divided at regular intervals by septa named Krause's disks or membranes. The dark particles, with a small portion of clear substance at either end, are Bowman's sarcous elements, and the same dark particles are held by Brücke to be made up of still smaller uniaxial crystals named *disdiaclasts.*

Unstriated muscle, sometimes called *smooth* muscle, forms an important part of the walls of the blood-vessels, alimentary canal, and genito-urinary apparatus. It consists of bands which, by appropriate means, can be separated into long fusiform nucleated cells. The colour of unstriated muscles is paler than that of striated, but they are fairly well supplied with blood-vessels, and abundantly with lymphatics, both of which present oblong meshes.

Chemical characters of muscle.—The reaction of muscle is alkaline. The sarcolemma resembles elastic tissue, being unacted on by acetic acid, and resisting long boiling in water. It differs from elastin in being slowly dissolved when heated in dilute solutions of acids and alkalies. It is slowly acted on by the gastric and pancreatic ferments.

The *anisotropous,* or *dark* substance, is solid, and, though allied to the proteids, differs from them in not being affected by alcohol or by salicylic acid, both of which precipitate the proteids.

Muscle plasma.—The *isotropous,* or *light* substance of muscle, can be obtained by pressure at 0° C. from the perfectly fresh muscles of frogs, thoroughly

freed from blood by injection. It is a fluid of syrupy consistence, with faint alkaline reaction, which coagulates like blood plasma. The coagulating substance is a globulin named *myosin*. It forms and coagulates slowly at 0° C., but instantaneously at 40° C. Pure myosin is obtained by dropping muscle plasma into distilled water, when it coagulates in the form of little balls. It is a neutral substance, insoluble in distilled water, but soluble in water containing between five and ten per cent of NaCl. It decomposes peroxide of hydrogen.

Muscle serum is the liquid which remains after the separation of the spontaneously coagulating substance from muscle plasma. It is alkaline, and contains three proteids in solution, viz. casein, serum albumin, and an albumin coagulating at forty-five degrees centigrade.

Colouring matter of muscle.—The red colour of muscle is due to the presence of *histo-hæmatin*, which is in combination with the plasma and not with the dark substance. Its presence in the muscle may be shown by holding a thin section before the slit of the spectroscope after all blood has been removed by washing out the vessels with weak solution of salt.

When muscle is treated with cold water the whole of the constituents of the muscle serum are dissolved, and perhaps some of the anisotropous substance. The fluid is found to contain the *nitrogenous compounds*, kreatin, kreatinin, carnin, xanthin, hypoxanthin, and urea.

Non-nitrogenous constituents of muscle.—These are fats, glycogen, and inosite, with the volatile fatty acids and paralactic acid. The quantity of glycogen is about 0·5 per cent. Inosite $C_6H_{12}O_6 + 2H_2O$ is a non-fermentable sugar crystallising in large colourless monoclinic tables. It does not reduce Fehling's

solution, but colours it green. Muscle contains a trace of pepsin, and probably also of a diastatic ferment which has not been isolated. The proportion of water in muscle is about seventy-five per cent. The organic matters, chiefly albuminous, are about twenty per cent., and the salts make up the remainder, the phosphates and potassium salts being particularly abundant. There are about six times more salts of potassium by weight than of sodium.

Healthy muscle during life, even when at perfect rest, abstracts oxygen from the blood passing through it, in addition to the materials required for its nutrition, and gives off carbonic acid, though in less quantity than the oxygen absorbed. Even after death, or in excised muscle, O is taken up and CO_2 eliminated. The exchange of gases is greatly augmented during contraction.

Properties of muscular tissue.—The most important properties of muscular tissue are extensibility, elasticity, and contractility. The *extensibility* of muscle is the elongation it undergoes when it is stretched by a weight. The *elasticity* is the power of recoil which muscle possesses when it is either elongated or compressed. The *contractility* of muscle is the power it possesses of shortening when stimulated either directly or through the nerves.

Extensibility of muscle.—This is difficult to determine, but Donders has endeavoured to estimate it by supporting the fore-arm at the elbow, when at right angles to the upper arm, and then suspending a weight from the wrist, and, after allowing it to act for ten seconds, suddenly snipping the thread that attached it. The result obtained was that the elongation was precisely proportioned to the weight. The extensibility of muscle is essential to the movements of the bones, for since the bones are surrounded by muscles on all sides, if these were rigid no movement could occur;

but as it is, when one set of muscles contracts and draws the bone with them, their antagonists yield to a corresponding extent.

Elasticity of muscle. — The elasticity of muscles is small, but perfect. That is to say, a very small weight will extend a muscle, but when that weight is removed it returns exactly to its original dimensions. The elongation of a muscle is not in exact proportion to the weight extending it; but, according to Wertheim, the elongation diminishes, at first quickly, and then more slowly, in proportion as the weight increases, and the curve of muscular elasticity, instead of being nearly straight, resembles an hyperbole. The limit of elasticity of a muscle is soon reached, so that the gastrocnemius of a frog extended by a weight of 100 grms. will no longer return to its original length. Yet the cohesion of the same muscle is sufficient to resist a weight of about 250 grms. even after death, whilst during life the breaking strain is about a kilogramme, or 1,000 grms. The importance of the elasticity of muscle is considerable, for it is due to this alone that, notwithstanding the distance between its points of attachment may be considerable, it is sufficiently tense to prevent time being lost before contraction occurs. Moreover, it permits the muscle, when brought into sudden action, to act smoothly and uniformly without danger of tearing. That the muscles of the body are always in a state of slight extension is shown by the retraction of the ends of a divided tendon.

Contractility of muscle.—This is the property which muscular tissue possesses of shortening when stimulated. The question was formerly much discussed whether the contraction is due to a *vis insita*, as Haller termed it, or property of the muscle itself, or whether it is due to the action of the nervous system. But such a discussion has long since been recognised as

unprofitable. The nervous and muscular systems are in reality fused together, and in some of the lower animals one part of a cell may be nervous and another muscular. And although the contraction of muscle ordinarily takes place in consequence of an impulse propagated from the nervous system, there can be little doubt that if the nerve tissue could be entirely removed from a muscle, it would still contract on the direct application of a stimulus to it. There are indeed instances of muscular tissue, such, for example, as the fœtal heart and the allantois, which contract rhythmically, notwithstanding that there is a complete absence of any differentiated nervous system; whilst in curare a drug is known which is capable of paralysing the extremities of the motor nerves, whilst the muscles still remain capable of responding to direct stimulation.

The irritability or contractility of both striated and unstriated muscle is rendered much feebler by exposure to cold, but is at the same time much longer preserved. Thus, the gastrocnemius of a frog in winter, when detached from the body of the animal, and exposed, with some precautions against drying, to a temperature a little above the melting point of ice, will preserve its contractility and alkaline reaction for as long a period as ten days, whilst in summer the muscle may cease to respond to a stimulus within twenty-four hours. The same holds good of the heart of a frog, which will sometimes, in winter, continue to contract rhythmically after removal from the body for nearly a week, whilst in summer it ceases to beat in a few hours. This effect of cold is also observed in the muscles of the higher animals, though the time is relatively much shorter. In man the muscles lose their irritability after sudden death, as by hanging, very quickly, no trace being observable after the lapse of from three to seven hours. In some cases of disease it lasts longer; and a case is on

record in which, the cause of death being aneurism of the heart, the muscles retained slight irritability for twenty-seven hours after life was extinct. The muscles of the new-born child lose their irritability sooner than those of the adult, providing the two are maintained at an equal temperature; but the body of the infant, being of smaller size, loses its heat, if no precautions are taken to prevent it, more rapidly than that of the adult, and the muscles may hence appear, deceptively, to retain their irritability longer.

The order in which the several muscles of man lose their contractility is: first, the left ventricle, which ceases to respond to any stimulus about three-quarters of an hour after death; then the large intestine, then the small intestine; and, after a few more minutes, the stomach, the urinary bladder; and, about an hour after death, the right ventricle; about one hour and a half after death the œsophagus, the iris ten minutes later, and then the muscles of animal life, those of the trunk losing it before the members, and those of the legs before the arms. The right auricle, which Haller rightly designated the "primum movens" and "ultimum moriens," retains its irritability the longest.

Rigor mortis.—Immediately after death the irritability of muscular tissue increases, but it soon begins to diminish, and as soon as all traces of irritability have died out rigor mortis commences. In this state the muscles become hard and stiff, presenting many of the characters of contraction. It appears to be of invariable occurrence. The instances in which it has been considered to be absent, as in death by lightning, in hunted animals, and in asphyxia, have probably been cases where it has occurred very early or late, and has been overlooked. In cases of gunshot wound of the cerebellum it has succeeded spasm of all the muscles so quickly, that the body has kept the

kneeling or sitting position it occupied at the moment of death. Rigor mortis commences in the muscles of the jaws, then in those of the neck and trunk, and, generally, in those of the lower limbs before those of the upper, but occasionally the latter stiffen first. From observations made on a considerable number of subjects, Niderkorn has constructed the following table, which shows the time when the rigor mortis was complete :—

Eleventh hour after death	1	Seventh hour after death	11
Second ,, ,, ,,	2	Third ,, ,, ,,	14
Thirteenth ,, ,, ,,	2	Fifth ,, ,, ,,	14
Ninth ,, ,, ,,	4	Sixth ,, ,, ,,	20
Eighth ,, ,, ,,	7	Fourth ,, ,, ,,	31
Tenth ,, ,, ,,	7	Total	113

So that as a rule the rigidity of the body is complete from four to six hours after death. It usually sets in more rapidly when the body preserves more heat than usual, hence it is early in its appearance in those who meet with sudden death. And Brown-Séquard records a case in which rigor mortis was established in the jaws several minutes before the heart ceased to beat. On the contrary, cold retards its appearance.

Section of the sciatic nerve causes the muscles of the lower limbs to stiffen more slowly than when the nerve is uninjured. Paralysed limbs are earlier affected than the opposite sound ones, perhaps because the healthy nerves maintain some degree of tonicity and chemical activity. The injection of defibrinated arterial blood has been found to render the muscles once more supple after they have commenced to pass into the state of rigor mortis, but venous blood is inoperative.

The cause of rigor mortis is believed to be the coagulation of the myosin, and it is remarkable that the injection into the vessels of a rigid limb of a ten per cent. solution of common salt, which is known to

dissolve myosin, restores the limb to its original condition of suppleness. Muscle in the condition of rigor mortis is shorter, thicker, and of firmer consistence than before, resisting pressure and any attempt to elongate it. It ruptures with less facility. The muscular current of electricity disappears, or is reversed. Its reaction changes from the alkaline reaction of healthy living muscle to acid, which is attributed to the presence either of sarcolactic acid, which is an isomeric modification of lactic acid, or to that of glycerin-phosphoric acid, or of both.

Stenson's experiment.—The muscles can be thrown into a state resembling or identical with rigor mortis by arrest of the supply of blood, a fact originally noticed by Stenson. The first effect of the ligature of a vessel passing directly to a muscle is, that its irritability is increased; it then rapidly lessens, and finally the muscle passes into a condition of stiffness. In the earlier period of the action the muscle is capable of completely recovering itself after removal of the ligature from the vessel, but in the later stage the muscular rigidity is permanent.

Heat rigor.—The muscles of mammals pass into a state of rigor at a temperature of 48°—50° C., those of frogs at 40° C., and those of birds about the temperature of 48°—50° C.

Water rigor.—The exposure of muscle to the action of distilled water induces a condition of rigor, and even ordinary sea-water acts in the same way, as is seen in the crimping of cod.

Acid rigor.—The injection of one part of lactic or hydrochloric acid into the muscles of frogs produces rapid stiffening.

Idiomuscular contraction.—When a muscle is nearly exhausted, and a direct stimulus is applied to it, a swelling or local contraction is often observed, which is slowly propagated in the form of a wave from

the point stimulated to both extremities. It may be observed even during life, the most favourable situation being the pectoralis major of patients affected with phthisis or other wasting disease, in whom there is little subcutaneous fat. In such patients a smart tap raises a swelling which may be seen to extend over the whole length of the muscle at the rate of about 18 in. per sec. Akin to idiomuscular contraction is the "fibrillar contraction," or quivering of various facial muscles, which is often experienced in enfeebled states of health, and may sometimes be seen in the strongly developed gastrocnemii. The same occurs in the muscles of the tongue after section of the hypoglossal nerve.

Tonicity of muscle.—By tonicity is meant that property of muscles by which they preserve a certain degree of firmness and slight contraction, which is best seen in the sphincters. It appears to be under the influence of the nervous system, since it is lost as soon as the nerve distributed to a muscle is divided, the muscle immediately becoming flaccid and relaxed. It fulfils the important purposes of aiding the elasticity in preventing any loss of time in the execution of movements when muscle is called into play, and of rendering smooth and uniform the movements of the limbs by antagonising the contraction of the opposing muscles. It also serves to maintain the surfaces of joints in a state of coagulation. It passes, by insensible degrees, into those pathological conditions that are seen in contractures of the muscles in paralysis, and which are usually associated with organic changes in the muscle itself.

Muscle stimuli.—(1) *Nervous impulse.*—The normal stimulus of muscle may be propagated to it through a motor nerve from one of the higher intellectual centres, when it is termed automatic or voluntary; or from some other centre, when it is usually of a reflex nature. It differs from most other

stimuli in bringing *all* the fibres of the muscle into action simultaneously.

(2) *Chemical.*—Such as the mineral acids, which act promptly upon muscle even in the dilute state, though they require to be rather concentrated to affect nerve. Lactic acid and glycerin are said to act on muscle only in the diluted state, and on nerve only when concentrated. Neutral alkaline salts act equally on nerve and muscle, and upon both with much energy, whilst alcohol and ether act upon both comparatively feebly.

(3) *Thermic stimuli.*—If the muscles of a frog be exposed suddenly to a temperature of 28° C. they gradually shorten, the contraction becoming suddenly strongly marked at 30° C., and attaining its maximum at 45° C., at which temperature it easily passes into heat rigor. There is a difference between the smooth muscles of mammals and the striated muscles in their relation to warmth, for heat causes contraction of the latter and relaxation of the former. Striated muscle of the frog, cooled down to the melting point of ice, is rendered very excitable, and if it be then subjected to lower grades of cold still, it is stimulated to contract. The muscles of animals that have been artificially cooled preserve their excitability many hours after death.

(4) *Mechanical stimuli.*—A sudden blow or prick of a muscle excites a contraction, and if the shocks be sufficiently frequently repeated, tetanus is induced.

(5) *Electric stimuli.*—These will be considered under the head of nerve; but it may be remarked that an electric current passed transversely across a muscle is a much less powerful stimulus than when made to transmit it in the direction of its length.

None of the above-mentioned stimuli excite contraction in a muscle if their intensity is very gradually

and slowly increased or diminished. It is necessary that the change should be sudden. Thus, whilst sudden exposure to a high or to a low temperature induces contraction, no effect is produced if the temperature is gradually raised or diminished. So, too, when a constant electric current is made to traverse a muscle, contraction only takes place at the moment of making or breaking contact. No contraction occurs whilst a constant current of uniform intensity, however strong, is passing along the muscle.

Phenomena of contraction.—(1) When examined with the naked eye muscle is seen, in the act of contraction, to become shorter and correspondingly thicker. It is not difficult to show that there is but little change in volume, and that the loss in length is almost entirely compensated for by a gain in thickness; for if a portion of the body of an eel be placed in a vessel, the stopper of which is drawn out so as to form a narrow neck, and which is filled with water, if the muscles be made to contract by some stimulus, and there was either increase or diminution of absolute size, the water would rise or fall in the capillary neck, but the most exact researches show that the variation in the level of the vessel is almost inappreciable, and that if there is any change during contraction it is slight diminution, which certainly does not exceed $\frac{1}{1370}$th of the total volume of the muscle.

The maximum contraction of a muscle in a single contraction is about $\frac{1}{5}$th of its length, but in tetanus it may shorten as much as $\frac{1}{3}$rd of its total length.

(2) Under the microscope the distinction between the isotropous and the anisotropous substance becomes in the first instance obscured, so that the whole contents of one of the compartments of Krause presents a uniformly dim aspect; but when the contraction is more advanced or complete, the central transverse dark band becomes lighter, and the terminal portions of the

compartment darker, so that the dark anisotropous bands which seem to be the really active portion of the muscle appear to advance upon and absorb the clear isotropous bands, which are more watery, and in closer relation with the terminations of the nerves.

(3) Certain *chemical changes* take place in muscle during contraction, the most important of which are that four or five times more oxygen is used up, and more CO_2 is produced, the venous blood returning from muscle containing more CO_2, and more CO_2 being eliminated by the lungs. The muscles become more watery. The components soluble in cold water diminish, those in alcohol increase. The amount of glycogen diminishes. Acids are developed, especially a form of lactic acid which has been named the sarcolactic acid, glycerin-phosphoric acid, and carbonic acid, and the reaction of muscle becomes acid.

(4) A *sound* is emitted during the contraction of muscle which may be heard when a muscle is made to contract, either by the influence of the will or by any external stimulus. It is audible when the masseter muscles are strongly contracted, and also when the muscles of the thumb are contracted and the little finger is inserted into the ear. The number of vibrations is 19·5 per sec., but it is not this deep note that is heard, but the first octave, overtone, or harmonic above it, having 39 vibrations per sec. On throwing a muscle into continuous spasmodic contraction by the action of an induced current, the vibrations, and consequently the pitch of the sound, agree with the frequency of the shocks of the induction apparatus.

(5) The temperature rises. In the muscles of a frog tetanised for a few minutes a rise of temperature amounting to about 0·16° C. has been observed. In a single contraction its rise was from 0·001° to 0·005° C.

The increase of temperature that takes place throughout the whole body as the result of exercise is

essentially due to muscular action. During repose of the body much less heat is generated. Hence the liability to chills and colds when sitting in a draught, from which the system is quite protected during exercise. Less heat is generated during sleep than in the waking state, chiefly because the muscular system is in repose. Hence the necessity for additional clothing during this period. In animals rendered motionless by curare death occurs essentially from loss of heat. It seems natural that more heat should be disengaged when the muscles perform no work than when work is done by their contraction, but, according to Heidenhain, muscle in contracting so that it does work, as, for example, lifts a weight, gives out an amount of heat which, within certain limits, *increases* with the amount of work done. In tetanus, where no work is done, the more the muscle is stretched or weighted, the more heat, within certain limits, it disengages. In both cases the energy the muscles develop increases with the tension of the muscle. It is correct, then, to say that muscle stimulated and prevented from shortening, or doing work, generates more heat than if it can do work; but it is incorrect to say that the greater the amount of work done the less is the quantity of heat that is disengaged.

(6) During contraction the normal electrical current of muscle diminishes in strength, and even becomes reversed, constituting the negative variation of Du Bois Reymond.

(7) In contraction the elasticity of muscle diminishes, that is, it yields to a greater extent with the same weight in the contracted as compared with the uncontracted state. This circumstance affords an explanation of the "Paradox of Weber," viz. that a muscle in repose, and heavily weighted, will, when strongly stimulated, become longer than in the quiescent state, instead of shortening.

Wave of muscular contraction.—When a stimulus is applied to the nerve supplying a muscle, of sufficient strength to excite contraction, the fusion of the two tissues is so complete that the whole of the muscle is made to contract, strongly or weakly, as the case may be, but still simultaneously, and the same occurs if a current of electricity be passed from one extremity of the muscle to the other, so as travel through the whole length of the muscle ; but if the current be applied to one extremity only it can readily be shown, by the graphic method and the attachment of a succession of levers or tambours to it in the direction of its length, that the contraction travels as a wave with considerable speed from end to end. In the gastrocnemius of a frog the rapidity with which the wave travels has been determined to be from 4 to 5 metres per second, whilst in the arm muscles of man it is from 10 to 13 metres per second.

The most rapid movements that can be executed by muscles under the influence of the will, as in writing, elocution, or in musical performances, do not exceed ten or twelve contractions per second.

A single muscular contraction.—There is no short term in English to designate the sudden, short, and transient shortening which is termed by the French a *sécousse*, or shock, and by the Germans a *zuckung*, or convulsion. It is the response of the muscle to a single stimulus, and much interest is attached to a tracing taken of it with a myographion.* Such a tracing is shown in the adjoining cut (Fig. 10).

It will be seen that there are four lines. The lowermost at 1 exhibits an abrupt descent which indicates the moment at which the shock was applied. The next undulating line represents the vibrations of a tuning fork, each double vibration of which occupied

* *See* companion volume on "Physiological Physics."

$\frac{1}{100}$th of a second, and consequently constitutes a reliable and perfectly uniform measure of time. The straight line L is the basal line, and is made by the style or brush attached to the muscle on the cylinder when this is revolving and the muscle is at rest. The line

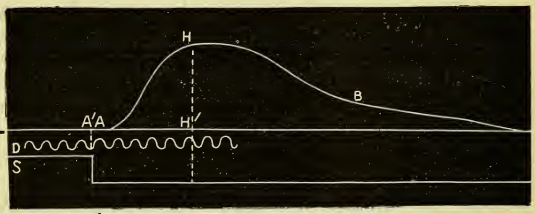


Fig. 10.—Tracing of a Single Muscular Contraction or Shock of the Muscle of a Frog.

S, Line showing at I, the point where it descends, the instant at which the stimulus of the electric shock was applied to the muscle; D, Tracing of the vibrations of a tuning fork vibrating 100 times per second; L, Basal line of muscle at rest; A'A, Latent period of contraction; AH, Period of contraction; HB, Period of relaxation.

AA'HB is the tracing of the muscle curve. It is divisible into three parts: (1) The latent period, A'A; (2) the period of ascent, A—H; (3) the period of descent, H—B.

The **latent period.**—Careful examination and comparison of time by means of the undulating line D renders it evident that the point A, at which the muscle begins to contract, and the curve to spring from the basal line, does not correspond with the point A' or I, which represents the moment at which the shock was applied, but that a short interval A'A intervened. This is the *latent period.* It lasts less than half a complete vibration of the tuning fork vibrating one hundred times in a second, and is therefore about $\frac{1}{200}$th of a second in duration. During this period the muscle seems to be

gathering itself together for the effort it is about to make, and we may suppose that some chemical change is taking place by which the liberation of muscular force is effected; and it is found that whatever tends to promote or facilitate chemical change tends to shorten the latent period, whilst all that acts prejudicially to chemical action, and impedes it, tends to lengthen it. Thus, the latent period is shorter in muscles that are slightly extended by a weight than in those that are absolutely quiescent, for in the latter case the chemical changes are at their lowest and have to be started, whilst in muscles doing a little work the changes are already in progress and are easily rendered more active. Again, the latent period is shorter at a moderately high than at a low temperature, and hence it is shorter in summer than in winter frogs. Again, it is shorter in mammals than in frogs; shorter when a powerful electric shock is applied than when it is feeble; shorter when the muscle is fresh than when it is exhausted by exercise, and, above all, shorter when it still forms part of the body of the animal than after its removal and manipulation. An additional argument is found in the circumstance that if a very feeble shock be applied to a muscle, a shock so feeble as to be insufficient to cause it to contract, the application of a second shock instantly induces contraction, the latent period almost disappearing. It seems probable in such case that the muscle is prepared for the effort by the shock first applied. The latent period is shortened by certain drugs, such as strychnia and veratria. In mammals it is very short, and is believed to oscillate about 0·008 sec., a little more or less. A very heavy weight appended to a muscle prolongs the latent period, and it is prolonged by curare.

Period of ascent.—The ascending portion of the line representing the muscle curve corresponds

with the contraction or shortening of the muscle. The rise is observed to be steep, and it can be shown by it that muscle contracts more rapidly at the commencement of its contraction than when it has nearly attained the maximum of its shortening, unless the muscle is heavily weighted, when the opposite conditions obtain.

Period of descent.—This is always slower or more prolonged than the period of ascent. It corresponds with the period of relaxation of the muscle, and, as in contraction, is more rapid at first than when the muscle has nearly resumed its ordinary conditions. It is succeeded by one or two secondary vibrations due perhaps to elasticity. When a muscle is lightly weighted, the descending portion of the curve does not reach the basal line, but when heavily weighted it may not only reach it, but descend below it, and then rise above it again. In the ordinary contraction of the gastrocnemius of the frog the relation in point of time of the period of ascent to that of descent is such that if the former occupies one-tenth of a second the latter occupies three-tenths.

Exhausted muscles have a longer latent period, contract more slowly and to a less extent, and have a longer period of relaxation. The curve is therefore lower and longer with the same stimulus.

Supermaximal contraction.—When, by the application of a series of stimuli, that is discovered which produces the utmost contraction of which a muscle is capable, by a continuance of stimulation a yet greater degree of contraction may, after a little time, in some cases, be obtained. This is called the supermaximal contraction.

The contraction of muscle is modified by temperatures, blood supply, previous stimulation, load, nature of stimulus, freshness, and nutrition.

Summation of stimuli.—As a general rule,

when a stimulus of moderate strength is applied to a muscle it contracts suddenly and completely, that is, to its fullest extent; but a stimulus may be applied to a muscle so slight that no contraction follows; if this feeble stimulus be quickly reapplied two or more times contraction ensues, or if the first feeble stimulus produces slight contraction, the second stimulus,

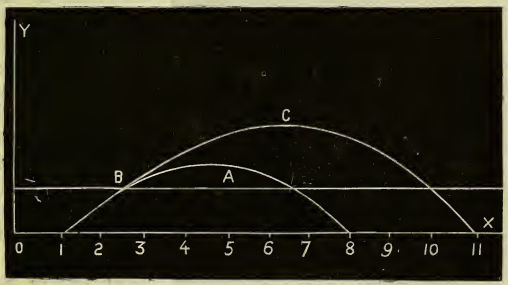


Fig. 11.—Summation of Two Stimuli.

though it may not be any stronger, excites a vigorous contraction. This gradually increasing action is termed summation by the Germans, and latent addition by the French. The interval of time between two successive stimuli may be as brief as $\frac{1}{1000}$th of a second and as long as ten seconds. Two stimuli, though removed from each other by an interval as short as the former of these periods or as long as the latter, are consequently clearly perceived by the muscle to be two, and the muscle curve produced by them differs in its characters from that produced by a single stimulus. If the two stimuli both occur within the latent period, or soon after the commencement of shortening, only one contraction will result, but it will be more vigorous than one alone. Thus, in Fig. 11

the first shock is applied at 0, and 0—1 = latent period, and BA 8 represents the curve that would be produced if that stimulus alone acted; but if now, when the muscle is just beginning to contract, a second stimulus is applied at B, the second contraction superimposes itself upon the first, and the stronger contraction BC 11 follows. The excitability of a muscle seems to increase when a succession of stimuli are applied, for it is possible to apply to a muscle a shock of such feeble intensity that no contraction follows, but if several such shocks are applied consecutively, a vigorous contraction may be induced. Thus it is seen in Fig. 12 that the application of the first two shocks was not followed by any contraction; the third, however, produced a slight rise in the myographic tracing, the fourth a distinct but slight muscular contraction, whilst the three

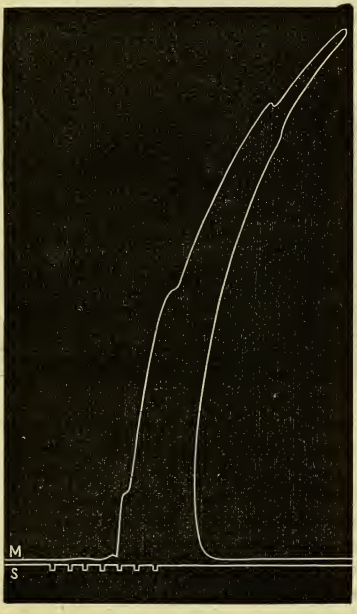


Fig. 12.—Muscle of Lobster.
Indications of seven electric shocks of equal intensity.

following shocks caused the muscle to contract energetically. Hence it appears that when successive and equal stimuli are applied they add themselves together and produce a much more powerful effect than either of them singly.

Secondary wave.—If a muscle to which a light weight is attached be thrown into tetanus and then left, it suddenly elongates, but soon begins again to contract without the further application of a stimulus. This contraction is termed the "secondary wave," and it is necessary, in order that it should appear, that the muscle should be very fresh and the weight light.

Contraction remainder.—When a muscle is much exhausted, and especially if not weighted, it may not fully return to its former condition, and the point of the lever will not descend to its original level, exhibiting what is then termed a contraction remainder.

Tetanus.—Tetanus is the fusion of a series of successive contractions into one continuous contraction. It occurs when stimuli are applied so rapidly that the muscle has not time to relax between the times of application of two consecutive stimuli. The number of stimuli required to throw a muscle into tetanus varies greatly in different instances. Thus, in the case of the pedal muscle of the snail, tetanus results even



Fig. 13.—Incomplete Tetanus; the undulation of the successive shocks being still perceptible.

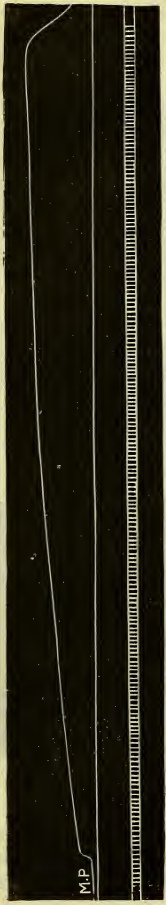


Fig. 14.—Complete Tetanus; the successive shocks are fused into one continuous line.

when the interval between two shocks is as much as ten seconds; two shocks per second are sufficient to throw the striated muscle of the tortoise into tetanus; the rapidly vibrating muscles of the insect require 300, of the bird 100; the gastrocnemius of a frog requires twenty-seven, and the pale muscles of the rabbit a very much greater number; the striated muscles of man require forty, the unstriated two. In the graphic tracing of tetanus the contractions caused by successive stimuli are seen to be superimposed, till at length a maximum height is observed, which is preserved as long as the stimulation is continued till exhaustion occurs, when the line suddenly falls. So long as the line, though high, presents undulations, the tetanus is said to be incomplete (Fig. 13); but when the tracing of the muscle forms a uniform line (Fig. 14) then the tetanus is complete. Before tetanus is established, when the number of excitations is considerable, there is generally one contraction, followed by relaxation. This is named the initial contraction; but instruments have been devised by means of which 22,000 stimuli can be applied in a second, and it is then said by

some that no initial contraction occurs, the muscle passing at once into tetanic spasm.

Action of curare on muscle.—Curare, or woorara, is the arrow poison of the South American Indians, and is remarkable for its power of rendering even large and powerful animals motionless, when introduced into their blood. In small doses it increases the irritability of both nerve and muscle, but in large doses it primarily affects the intramuscular terminations of the motor nerves without impairing the functions of the sensory nerves.

That curare acts on the intramuscular terminations of the motor nerves is shown by applying a ligature tightly to the leg of a frog beneath the sciatic nerve, so that whilst the circulation is wholly suppressed in the limb, the nerve is uninjured. On injecting curare into the skin of the back, it is absorbed and acts on all parts except the leg round which the ligature has been drawn. If either a mechanical, chemical, thermal, or electrical stimulus be now applied to any of the nerves distributed to other parts than the ligatured limb, no movement will take place, but if a stimulus be applied to the *roots* of the sciatic nerve of the ligatured limb, which, being above the ligature, have evidently been exposed to the action of the poison, the muscles still respond readily enough, showing that although the poison has acted on the peripheric extremities of the nerves in other parts of the body, it certainly has not acted on the nerve trunks or roots. In the same frog it may be shown that curare does not act on sensory nerves nor upon the nerve centres, for if one of the legs not ligatured be pinched, contractions are observed in the ligatured limb, whilst the rest of the body remains in complete repose.

A warm-blooded animal, to which a sufficient dose of curare has been administered, soon becomes incapable of voluntary movement; the striated muscles,

with the exception of the heart, cease to respond to nervous impulses, and hence, although the heart continues to beat, death takes place owing to failure of the respiratory movements, and consequently asphyxia. In the case of a frog similarly poisoned, life is not destroyed, because this animal is capable of respiring by the skin, but it is still wholly deprived of the power of spontaneous movement. The life of the warm-blooded animal can, like that of the frog, be preserved if artificial respiration be maintained, and in that case it is found, that although no stimulus applied to the nerves supplying muscles will occasion contraction, yet that the muscles themselves respond readily enough to stimuli when directly applied.

Further evidence of the irritability of the muscles being a property of the tissue itself and not dependent on the nerves, is derived from the fact that after section of a motor nerve, the peripheric portion degenerates and ceases to respond to stimuli, whilst the muscle long preserves its contractility. And, again, muscle and nerve are differently acted on by ammonia, for a nerve dissected out for some distance above its entrance into a muscle, and dipped in a solution of ammonia, provokes no contraction in the muscle to which it is distributed, but if ammonia be allowed to act on muscle immediate contraction results.

In large doses the inhibitory fibres of the vagus are paralysed, and the heart consequently beats more frequently. Curare produces little effect when taken into the stomach, because as fast as it is absorbed it is excreted by the kidneys; but if the ureters are tied, the poison accumulates in the blood, and the usual effects are observed.

Two muscles, of which one is under the influence of curare, contract nearly equally on opening and closing a constant current of electricity, but when exposed to the intermittent action of induced currents

a stronger current is required to excite the curarised or "enervated" muscle. The non-curarised muscle behaves with the induced current in the same way as if the current were applied to the motor nerve. This difference in the effect of constant and induced currents is utilised by electro-therapeutists to decide whether a paralysis is due to some peripheric lesion of the motor nerve, or results from lesion of the nerve centre. For if a motor nerve be divided or is suffering from peripheric lesion, which amounts to the same thing, it degenerates towards and up to its peripheric termination, but this does not occur where the lesion is in the nerve centres. If, therefore, in the course of from eight to fifteen days after the occurrence of the paralysis, the irritability of the paralysed muscle to the induced current is preserved, it is concluded that the nerve centres are affected, but if the irritability is abolished or seriously diminished the lesion is peripheric (Nuel).

Action of some other poisons.—Chloroform, ether, and chloral retard the whole process of contraction; oxide of carbon, which at ordinary temperature has no action on muscular irritability, abolishes it at a pressure of five atmospheres.

Some poisons have a remarkable influence on the muscle curve; thus, *veratria,* the action of which has been studied by V. Bezold, produces the following effects. If one or two drops of a very dilute solution of veratria be injected into the lymph sac of a frog, and the condition of the animal be examined in the course of a quarter of an hour, it will be found that when it is incited to spring the movement is rapidly and vigorously accomplished, but that on alighting, instead of the legs being under the belly and prepared for a fresh spring, they are extended behind, and are only slowly drawn up. The characteristic features of the movement are rapid and powerful contraction with very slow

relaxation. The form of the muscle curve from a frog poisoned with veratria explains the reason of this condition. The ascending part of the line is precipitous, and ends when it has reached a considerable height. The summit of the curve proper is not remarkably prolonged, and it is often succeeded by a descent; but at this point the effect of the poison becomes characteristic, for the curve suddenly ceases to fall, and rises to an altitude far above that attained by the primary contraction. When the "veratria contraction" has reached its maximum it begins to decline, and then gradual relaxation continues with diminishing speed till the base line is regained. The whole contraction resulting from a single stimulation may occupy 5″ to 15″, or longer. The effects of heat or cold on the form of the two parts of the curve have been studied by Brunton and Cash, who show that in regard to the veratria curve the effect is the same as in the unpoisoned muscle, cold lengthening and sometimes lowering the altitude, while heat shortens and increases the altitude.

Necessity for free supply of blood.—The capability of muscle to respond to nerve stimulation, whether direct or indirect, is diminished by fatigue, and abolished by exhaustion, and the same effect is produced by any means preventing the supply of blood to it, whether by pressure or ligature of the artery of the limb, by the injection into the vessels of any fine powder which obstructs the capillaries, or by the application of an Esmarch's bandage. On re-admission of the blood, if the supply have not been too long cut off, it is soon recovered. The muscle does not lose its irritability in anæmia, for it may still respond to direct stimuli, but nervous impulses can no longer be communicated to it. The heart, however, seems to be differently affected, since it stops instantly after ligature of the coronary arteries. In frogs the whole

of the blood may be replaced by solutions of common salt in the proportion of six grains to the litre. Yet voluntary and reflex movement, and the excitability of the muscles, may be preserved for many hours. When all signs of irritability have ceased, this property of muscle may be restored by the injection of warm defibrinated blood into the vessels. In the dog restoration may take place six hours after the last signs of irritability have vanished, and in pigeons after one hour. Speaking generally, muscle can live and contract independently of the rest of the body, but it requires oxygen for the maintenance of its activity, and it is necessary that the products of its waste should be removed; both of these conditions are fulfilled by the blood current.

The changes of the blood stream in muscles through stimulation of their nerves. —This subject has been especially investigated by Sadler and by Gaskell, and their observations show that when muscles are made to contract by stimulation of their nerves, the flow of blood returning from them is quickened. If tetanus be induced, there appears a spurt-like quickening of the stream followed on further contraction by an almost complete cessation of flow, which then again steadily increases in volume; at the end of the tetanus the rate of flow sinks a second time for a moment, and then rises again in the course of some seconds to a new maximum, from which it falls slowly to near the value it possessed before the stimulation. Upon the whole, there is an increased flow of blood through a muscle in contraction, and the explanation appears to be, that when the muscle is made to contract by the direct stimulation of motor nerves, its arteries are at the same time made to dilate by the direct stimulation of dilator nerves. Section of the nerve distributed to a muscle causes a great increase in the

rate of blood-flow through the muscle, which attains its maximum in from twenty to forty seconds after the section, and which has entirely disappeared in from two to four minutes after the section, whether the animal is anæsthetised or unanæsthetised, or curarised.

Small dilatations have been observed in the small vessels and capillaries of muscle in which blood may accumulate, and a supply of nutriment and of oxygen is thus afforded which can be drawn upon during prolonged effort.

Sensibility of muscles.—Muscles are supplied with sensory nerve fibres; indications of pain are observed when they are cut, pinched, bruised, or otherwise injured. The pain that accompanies cramp is well known, and is probably due to compression of sensory nerves. The sensation of fatigue is perhaps attributable to the retention of the products of disintegration, such as sarcolactic acid in the tissue, and their action on the sensory nerves. The muscular sense or sensibility by which we judge of the position of the various parts of the body and estimate weights, will be referred to when tactile sensibility is discussed.

Effects of nerve lesions on muscle.—In the course of three or four days after lesion of a motor nerve, the muscle supplied by it reacts less powerfully to both direct and indirect stimulation of the nerve. This period is succeeded by one in which constant currents act more powerfully whilst induced currents are almost inoperative. There is also increased excitability for direct mechanical stimuli. This occurs about the seventh week, and from this time it gradually sinks up to the sixth or seventh month, when it disappears altogether. Under the microscope fatty degeneration appears about the second week, and gradually progresses until complete atrophy results (Landois).

Work done by muscle.—The work done by a muscle is estimated by multiplying the weight raised by the height to which it is raised. If there is no weight to be lifted no work is done, and, in a similar manner, if the weight is so heavy that it cannot raise it at all, no work is done. If the weight be gradually increased from a minimum it is found that the work done steadily increases up to a certain point; when this is passed the height to which the weight can be raised diminishes, and the work done diminishes. Thus, in one experiment Weber found that with

Weight attached to muscle, in grammes.	Height to which weight was raised, in millimetres.	Work done, in gram-millimetres.
5	27·06	138
15	25·01	376
25	11·45	286
30	6·03	220

From which it appears that most work was done in this case with a weight of 15 grammes.

Absolute muscle force.—This is the weight which a muscle stimulated to the utmost is just unable to raise, so that it retains its natural length before being weighted, though at the same time it does not elongate at the moment of stimulation. As a means of comparison of the absolute muscle force of different muscles, it is estimated on 1 square centimetre of the mean transverse section. Now, the mean transverse section is obtained by dividing the volume of a muscle by its length, and the volume equals the absolute weight of the muscle in question, divided by the specific gravity of muscle, which is equal to 1·058. The absolute force of 1 square centimetre of frog's muscle is thus estimated at 2·8 to 3 kilogrammeters; and for the same area of human muscles it is about 8 or 9 kilogrammeters. The greatest exertion of a man, reckoned at eight hours per diem, is calculated to be

about 10 kilogrammeters per second, or 300,000 per diem. One horse-power equals seven times this amount.

Electrical condition of a muscle at rest.—If a pair of unpolarisable electrodes are applied to the surface of an exposed but uninjured muscle, little or no evidence of electrical tension is afforded; but if any part of the surface is bruised, cut, or otherwise injured, that part immediately becomes negatively electric, whilst the undamaged part is positively electric. It is difficult to prepare any of the ordinary skeletal muscles for this experiment, though the gastrocnemius of the frog can be exposed with least injury; but the heart may be employed, the electrodes being applied to it in diastole, or when its beats have been retarded by muscarin. If a long muscle be carefully removed from the body, the two ends cut away, and the electrodes applied, one to the outer longitudinal surface, and the other to the cut transverse surface, it will be found that the smooth outer surface is positive, and the transversely cut surface is negative, the strongest current being obtained when the electrode is placed on the middle or equator of the longitudinal surface, and the other on the centre of the cut surface. A current, therefore, passes *outside* the muscle from the longitudinal to the transverse section, and there must be a similar current *inside* the muscle from the transverse section to the longitudinal surface or section, or the electrical tension would soon be equalised.

No current is obtained if two symmetrical points of the muscle are tested, that is, if the electrodes are applied to two points of the longitudinal section equidistant from the equator, or to two points of the transverse section equidistant from the axis. Some experimenters believe that electrical currents *pre-exist* in quiescent muscles; others consider that electrical

currents are only generated when muscles have been injured, the injured part in dying becoming electro-negative, and the uninjured part positive. The currents are so far interesting that they only occur in living muscle, and disappear altogether when its excitability has vanished. When the excitability is only partially extinct, a fresh transverse section causes them to reappear, which Hermann explains as a result of new contractile molecules being exposed to the air, and, in undergoing oxydation, becoming the source of fresh electrical manifestations. The currents demonstrated in the foregoing mode are, it must be remembered, only *derived currents;* much more energetic ones probably exist in the muscle itself, for when we apply two unpolarisable electrodes connected by a wire to the surface of a muscle, we derive a fraction only, and probably only a very small fraction, of these currents from a few superficial contractile molecules, yet the electromotor force of the muscles of a frog amounts to about one-tenth of a Daniell's cell, and that of mammals is nearly the same.

Electrical manifestations of muscle in action.—The simplest case is presented in the application of a single stimulus to a curarised muscle, the fibres of which are parallel, and the length of which does not exceed that of the fibres themselves. The region excited develops for a very short space of time a negative electric tension which disappears whilst the next segment of the muscle becomes negative, and so on towards both of its extremities. The rapidity of propagation of this negative wave is the same as that of the propagation of the muscular wave, or three meters per second, and as it precedes the contractile wave, coincides with the latent period of the contractile energy. It appears in the region stimulated at the very moment of excitation, and is consequently the first appreciable phenomenon of muscular

excitation, the first sign of intramolecular change. It shows that during the latent period the contractile substance is by no means at rest, but is the seat of very important molecular phenomena (Nuel). Any portion of muscle to which a stimulus is applied is negative to the non-stimulated portion. The duration of the negative wave is about 0·004 sec., which gives a length of wave of about 12 mm. The term, *current of action*, has been applied to the current produced by the negative wave, and its electromotor force may, like that of the current of repose, rise as high as one-tenth of a Daniell's cell.

When a galvanometer is used to demonstrate in the usual way a current of repose in a muscle, if the muscle be tetanised either directly or indirectly, the needle swings back towards or beyond zero. This is the negative variation of Dubois Reymond, of the current generally admitted to exist in quiescent muscle.

Unstriated muscular tissue.—The physiological investigation of unstriated muscular tissue is rendered difficult, on account of the difficulty of obtaining a mass of it in an isolated state, its inaccessibility, and the circumstance that it is often arranged in alternating layers, which have a different, if not, as in the case of the intestinal wall and iris, a precisely opposite action. In experimenting on the retractor penis of the horse, dog, and some other mammals, where the fibres form a mass of considerable size, almost pure, and easily accessible, Sertoli has found that this example of smooth muscle retained its excitability for an extraordinary time (with proper precautions to prevent loss of heat and desiccation), contracting, in response to stimuli, five, six, or even seven days after removal from the body. At a temperature of 104° F. it soon became fatigued, and lost its irritability. Its most remarkable power was found to be that of executing spontaneous movements even when

removed from the body, the contractions lasting from two to six minutes, and the degree of contraction being about one-fifth of the total length of the muscle. The intermissions were short. The movements cease in deep narcotism, in anæmia, and with deficient supply of oxygen. Direct stimulation with a constant current caused elongation with complete cessation of spontaneous movements when the current was passing. The application of an induced current caused contraction. The graphic tracing resembles that of striated muscle. but exhibits a latent period of 0·8 second, which is nearly 100 times longer than that of striated muscle, and a period of contraction lasting from 90 to 120 seconds. The contraction is moderately rapid, the relaxation at first slow, then more rapid, and finally very slow. Tetanus supervenes when the shocks do not succeed each other more rapidly than at intervals of one in five seconds, or twelve per minute.

It has been pointed out by Gaskell that muscular tissues exhibit three different modes of responding to stimulation according to their structure. These modes may be expressed by saying that some muscles possess essentially the power of tonic contraction, others the power of rhythmical contraction, and others that of rapid contraction; the three forms may be exemplified by a comparison of the tetanising action of a strong interrupted current upon a strip of muscle from the bladder of a tortoise and from the heart of a tortoise, with the ordinary tetanus curve of the gastrocnemius of the frog. The unstriped muscle of the bladder contracts slowly after a long latent period, the contraction increasing steadily in force during and even after the cessation of the tetanising current, and then the strip returns with excessive slowness to its original length; in other words, we see a prolonged tonic contraction as the result of the stimulation. With striated muscle we

have the curve of tetanus composed of the superposition or fusion of a series of rapid contractions. The cardiac strip gives a curve which is intermediate between the two, and may be described as consisting of a long-continued tonic contraction upon which a number of rapid contractions are superimposed. These separate rapid contractions never succeed one another so quickly as to fuse together. When exhausted, however, it contracts with a tonic contraction like unstriped muscle.

Arrangement and application of muscles in the body.—The muscles constitute nearly one half of the total weight of the body, and they are divided into several groups, according to their mode of action. Some have no definite origin and insertion, but surround cavities, and form the walls of tubes, as in the case of the muscular walls of the alimentary canal, of the bladder and uterus; the coats of blood-vessels, glands, ducts, and lymphatics, all of which have for their purpose the contraction of the spaces they bound, and the onward movement of their contents. Others surround the orifices of the various apertures of the body, and are termed sphincters. Other groups of muscles have one attachment to some fixed point, and the other in a soft tissue, the movement of which they effect; such, for example, is the azygos uvulæ. And others again, which are by far the most numerous, have two points of attachment into bone, and with the bones act as levers. Prof. Haughton has pointed out that in most kinds of labour which are effective and usually employed, almost all the muscles of the upper and lower extremity are exerted, together with the muscles of the lumbar and dorsal vertebræ. He takes the work of the Oxford or Cambridge eight-oar boat as an example of extreme muscular exertion, and shows that the work done by each man is nearly 4 foot-tons per minute. The average daily work of a

labourer is about 400 foot-tons, accomplished in 10 hours. The oarsman, therefore, performs in one minute the hundredth part of a fair day's labour, and if he could continue to work at the same rate he would finish his task in one hour and forty minutes, instead of the customary ten hours. The work done, therefore, in rowing one knot in seven minutes is, while it lasts, performed at a rate equal to six times that of a hard-worked labourer. The most effective mode of employing human labour is to make a man lift his own weight through a height for many hours. This may be accomplished by making a labourer step into an empty barrow, and by his weight hoist a full barrow through a certain distance. Arrived at the bottom, he steps out of the empty barrow, and climbs a ladder to his original station, and again descends. The work capable of being thus done was found to be 910 foot-tons, which, expressed in foot-pounds per ounce of muscle per minute = 7·389 foot-pounds. From other experiments, Haughton arrived at the conclusion that the coefficient of contraction of living muscle, such as the biceps, was about 95 lbs. per square *inch* of cross section.

Joints and joint movements.—Joints result in some instances from the necessity of allowing for the enlargement of the contents of cavities, as in the case of the cranium. In such joints, termed synarthroses, there is no movement, but in other cases they exist to enable parts to move more or less freely upon one another. The movement is sometimes very slight, as in the articulation of the pelvic bones with each other or with the sacrum, and the attachment of the bones of the vertebræ to one another. These are termed amphiarthroses, and they combine great strength with some degree of movement. The other joints are those which are intended to permit free movement, and which exist between the extremities of the bones of the limbs. In those which are termed diarthroses the

opposed surfaces of the bones are covered with cartilage, over which, as well as over the inner surface of the ligaments binding them together, is originally a thin membrane resembling the serous membranes, but differing from them in the character of its secretion, which is glairy, and adapted to lubricate the surfaces, named synovia. The membrane has hence been called the synovial membrane. As soon as the joint is used, the cells covering the cartilage are worn away and are not replaced; and, in the adult, the membrane, which is composed of a matrix of delicate connective tissue with elastic fibres, and lining membrane of flattened epithelial cells, appears to terminate at the margin of the cartilage by a zone of polygonal endothelial cells. Processes are often given off from the inner surface of the membrane, which, projecting into the joint, contain fat and vessels. The *synovia* is a colourless viscid fluid, containing mucus, albumin, and traces of fat and salts. It is diminished in quantity after active exertion, when it also becomes thicker in consistence owing to increase of the mucus.

The movable joints are divided into the *arthrodia*, where two plane surfaces are in apposition, like the os calcis and cuboid; the *ginglymus* or hinge joint, like that of the elbow or knee; the *enarthrodia*, or ball-and-socket joint, as the hip and shoulder joints; and the *rotatoria*, as in the radio-ulnar articulation and the articulation of the axis and atlas.

Positions and Movements of the Body.

The bones constitute a system of levers or rigid bars, which are acted on by the muscles and effect the movements of the body. The different kinds of levers, in which the fulcrum, the weight, and the power are respectively in the middle, are all represented in the body. An example of the first order of lever is found in the muscles moving the head forwards and

backwards on the vertebral column. Thus, in the case of the backward movement, the rectus capitis posticus minor, amongst other muscles, represents the power, the occipito-atlantal articulation is the fulcrum, and the fore part of the head is the weight to be raised. Other examples of this form of lever are found in the movement of the trunk on the pelvis, of the foot on the leg, and of extension of the fore-arm. An example of the second form of lever, in which, as in the first form, great power can be exerted by lengthening one arm of the lever, is found in the gastrocnemii when acting on the foot in such a manner as to raise the body. The force is here applied to the os calcis, the fulcrum is the point of contact of the ball of the great toe with the ground, and the body is the weight to be raised. The third form of lever, in which the power is in the middle, is by far the most frequent, because, with some sacrifice of power, there is great gain in rapidity of action; and, as a rule, rapidity is required rather than strength. It is to be seen in the biceps of the arm and leg, the deltoid and brachialis anticus. In every position of the body, except lying, muscular effort is required, though the number of muscles brought into play in the sitting position is much less than in standing.

Standing.—In this position of the body it is necessary that a line dropped from the centre of gravity, which is situated about the second sacral vertebra, should fall on the area covered by the feet, or the space between them, and that the body, as a whole, in spite of its numerous articulations, should be kept rigid. The slightest inclination to right or left, forwards or backwards, tending to cause the centre of gravity to fall outside the surface covered by the feet, is counterbalanced by the action of opposing muscles, which serve to restore the equilibrium, and that these really act is shown by the impossibility of

setting a dead man, or one who has only fainted, on his feet.

Sitting.—In this position the body rests on the tubera ischii, on which a rolling movement, forwards and backwards, can be made. The body and head are maintained in the vertical position. If the forward movement be carried so far as to allow the centre of gravity, which is in front of the tenth dorsal vertebra, to fall in front of the two tubera ischii, the body must be supported by resting the arms on some solid body, or the thighs must be supported. If the body be inclined far backwards, the coccyx may help in sustaining it, whilst the psoas-iliac muscle, pectineus, and other muscles contract, and fix it upon the thigh, and the quadriceps extensor femoris again fixes the thigh upon the leg; the leg is then either raised and forms the long end of a lever, of which the fulcrum is at the tubera, and the weight is the trunk; or the flexors of the leg act and press it against the support.

Walking.—Walking is the horizontal forward movement of the body, by the alternate use of the two lower limbs and with the minimum of exertion. The leg resting on the ground is the "active" leg; the other, which is swinging through the air, is the "passive" leg. The following are the two phases of the act, as given by Landois. In the first, the active leg stands vertically, the knee joint slightly bent and immediately beneath the centre of gravity; the passive leg is completely extended, and rests only with the point of the great toe on the ground. In this position a rectangular triangle is formed, of which the active leg forms the hypothenuse. In the second phase, the active leg inclines forwards, the body is maintained at the same height, and, in order to accomplish this, the active leg is elongated by fully straightening the knee, and by raising the heel from the ground so that the foot rests

on the ball, and ultimately on the tip of the great toe. During the period that the straightening and forward inclination of the active leg is completed, the passive leg leaves the ground with the tips of the toes. The knee is now somewhat bent and executes a pendulum-like swinging movement forwards, and comes to occupy a position as far before the active leg as it was previously behind it; the sole of the foot is placed flat on the ground, and the position of the centre of gravity is now so altered by the lateral movement of the body as to act through this, which is now become the active leg, and is slightly bent at the knee, and the first of the two phases recommences. The lateral movement of the body, made with the object of shifting the centre of gravity to the active leg, is accomplished by the glutæi and tensor fasciæ femoris, and in persons of heavy build, and in women who have naturally broad pelves, gives rise to more or less of a waddling gait. In moderate walking the body is inclined slightly, in fast walking strongly forwards. During the swinging movement of the leg, the body executes a slight rotatory movement on the head of the active femur; but this is to some extent compensated by the arm of the same side swinging in the opposite direction, whilst that of the opposite side moves with the swinging leg. As the rapidity with which the swing of the leg is accomplished varies with its length, it is apparent that each person must have a certain natural rapidity of walk, but the duration of each step depends, in addition, on the time that both feet are simultaneously in contact with the earth, which is dependent on the will. In very fast walking this period is nil, as the moment that the active leg touches the ground the passive one is raised. The length of the step is about two and a half feet and is longer in proportion as the length of the hypothenuse of the passive leg surpasses the opposite side

of the triangle formed by the active leg. Hence, in striding, the active leg is shortened by bending at the knee, and the body is carried lower.

Running differs from walking in the circumstance that for a short interval both feet are off the ground together, and the body is in the air. The active leg is more bent at first, and is then straightened with a force that corresponds with rapidity of movement.

Leaping.—In leaping, the hip, knee, and ankle joints, previously bent in opposite directions, are suddenly extended, both leaving the ground at the same time. The muscular effort made is more than is sufficient to straighten the limbs, and an impulse is therefore imparted to the centre of gravity of the body, which is thus propelled in the manner of a projectile in the mean direction of the joints which are thus extended.

CHAPTER XIV.

THE NERVOUS SYSTEM.

Nervous tissue is composed of nerve cells and nerve fibres, which are processes given off from the cells. In the central parts of the nervous system, such as the brain and spinal cord, the cells are accumulated in large numbers, and are imbedded in a substance variously termed neuroglia, reticulum, supporting tissue, and polio-synectic tissue.

The cells and the fibres are organically continuous with one another, and impressions affecting the one are propagated to the other; but these functions are so far different that the nerve cells act as receivers of impressions and as originators of impulses, whilst the nerve fibres are the conductors which transmit

impressions from the periphery, towards the cells, or from the cells to the periphery. The parts of the cerebro-spinal nervous system are the spinal cord and its continuation upwards, the medulla oblongata, the pons, a chain of ganglionic masses situated at the base of the brain, the cerebrum, the cerebellum, and the various nerves that originate in or are indirectly connected with these several parts. Before describing the functions of the centres of the nervous system it is necessary to make some general observations on the characters and properties of nerve tissue in general, and of the mode in which it can be excited to action.

Chemistry of the nervous system. — The nerves are essentially composed of protoplasm, that is to say, of a proteid substance, and of fat compounds. The grey matter which forms the outer part of the brain and the inner part of the spinal cord, contains a larger proportion of water than the white substance, the proportion being 81·6 per cent. in the grey substance, and 68·4 per cent. in the white. When dried at a gentle heat the grey nervous matter yields 55·4 per cent. of albumin and glutin, 17·2 of lecithin, 18·7 of cholesterin and fats, 6·7 of extract insoluble in ether, and 1·5 parts of salts. The dry substance of the white matter of the brain and spinal cord yields only 24·7 of albumin and glutin, 9·9 of lecithin, 51·9 of cholesterin and fats, 3·3 of substances insoluble in ether, and 0·6 of salts. Of the salts, those of potassium and phosphoric acid greatly preponderate. The albuminous or proteid compounds of nervous tissue in part resemble myosin, in part casein, and a form of globulin. The albuminoids are nuclein and neuro-keratin. The principal mass of the brain is considered by Liebreich to be composed of protagon, which is a proteid containing both nitrogen and phosphorus. Others regard protagon as composed of lecithin, which contains the phosphorus, and cerebrin. Cerebrin

$C_{17}H_{33}NO_3$ is a glucoside, and is chiefly contained in the white substance. Both cerebrin and lecithin are soluble in hot alcohol and ether. The extractives include, amongst other substances, xanthin and hypoxanthin, kreatin, inosite, leucin, and lactic acid. The reaction of nervous tissue at rest is either neutral or feebly alkaline, but when excited to action and after death it becomes acid, apparently, as in the case of muscular tissue, owing to the development of lactic acid.

The *cohesion* of nerve fibres is very small, but when bound together with connective tissue to form nerve cords they present considerable resistance to rupture. The nerves possess little or no *elasticity*, so that when cleanly divided the ends remain in apposition.

Nerve stimuli.—Nervous tissue may be regarded as matter in a very unstable state of chemical composition, so that the application of various external agents, named *stimuli*, causes it to readily undergo decomposition. These, as in the case of muscle, may be mechanical, chemical, thermic, electric, or they may be waves or impulses transmitted from other cells. The effect of the stimulus is to alter the composition of the cell substance and to liberate force. A certain suddenness of application is requisite for any stimulus to excite the nerve, and that if it be applied with extremely gradual increments of intensity, beginning from 0, it may be augmented till the nerve is destroyed without producing any noticeable effect.

Mechanical stimuli.—The mechanical stimuli acting upon nerves may be of various kinds, such as a blow, or succession of blows, pressure, traction, puncture, and division. If these act on a sensory nerve they give rise to impulses, which, travelling centripetally along different nerves, produce sensations of characteristic nature, which experience enables us to refer to their cause, and to the particular nerve excited. If they act on a motor nerve the impulses

travelling centrifugally excite contraction in the muscle they supply, or secretion in the gland to which they are distributed. The smallest mechanical stimulus which can be perceived is that produced by the fall of 900 milligrammes through a height of one millimeter. Slight pressure or extension of nerve fibres increases their excitability, whilst strong stimuli exhaust them. The increased excitability in the former case soon disappears, and in the latter case, though the part struck or injured loses its excitability, the whole nerve is not exhausted, since the application of the stimulus at a lower point produces nearly the same effect as before. When persistent pressure is made upon a motor and a sensory nerve simultaneously, the excitability of the motor nerve is first lost.

Thermic stimuli. — A sudden elevation of temperature or a sudden depression acts as a stimulus to nerves. Within moderate limits heat augments and cold depresses their excitability. Exposure of the nerves of a frog to a temperature of 50° C. (122° F.), after first exalting, quickly abolishes the irritability of nerve. Nerves which have been gradually frozen and slowly thawed preserve their irritability for a long time.

Chemical stimuli.—These act upon the nerves when of sufficient strength to effect a rapid alteration in their composition. The motor nerves are more readily acted on than the sensory, in which respect chemical differ from thermic stimuli, which more readily act on the motor nerves. Rapid withdrawal of water from a nerve, as by folding it in blotting paper or exposure to a very dry air, acts as a stimulus to it. Strong solutions of the neutral salts of the alkaline metals constitute stimuli; common salt, however, acts only on the motor nerves. Free acids, with the exception of phosphoric acid, the alkalies, many organic acids, and most of the salts of the heavy

metals, act vigorously. Much stronger solutions of the acids are required than of the alkalies; the latter are still effective when in strength not exceeding 0·5 per cent. Such dilute solutions first augment the excitability and then depress it. Dilute alcohol, ether, chloroform, bile and the biliary salts, and sugar, all act as stimuli. They usually first induce convulsions and then cause death of the nerves. Lime-water, carbon bisulphide, and some others kill the nerve without exciting convulsions. Carbolic acid, if applied to the spinal cord, produces spasms, but if to the nerves kills them without producing convulsions. The last-mentioned substances act as excitants to muscle when directly applied to it. Tannic acid acts neither on nerve nor muscle.

Physiological stimuli.—The nature of these is unknown, but they may act on the centripetal nerves, as in the various sensations, or on the centrifugal nerves, producing either motion, or the inhibition of motion, or secretion.

Electrical stimuli.—Electrical currents may be applied to nerves either in the form of the constant or of the induced current, and the effects differ in some particulars. As in the case of other stimuli, no effect is produced if either form of current be very gradually increased from zero. Sensations or muscular contractions only occur when the current is suddenly applied, stopped, or greatly increased or diminished in intensity. In the case of the *constant* current applied to *motor nerves*, contraction only takes place at the moment when the current, of which the nerve forms a part, is either made or broken. During its steady passage no contraction occurs when weak, but with a certain moderate strength of current the muscle may be thrown into permanent tetanus, a condition that is sometimes termed "galvanotonus." In the case of secretory and vasomotor nerves no effect is produced during the

passage of the current of uniform strength. Very little effect or none is produced when the current is made to pass transversely across a nerve. It must, to produce contraction, pass through it in a longitudinal direction, and the longer the portion the weaker is the current required to produce a given effect. A certain duration of the current is necessary; if it is briefer than $\frac{1}{10000}$ths of a second no effect follows. In the case of *constant* current applied to *sensory* nerves, the stimulating effect is also most marked at the moment of closing and opening the current, the sensation being comparatively slight during the passage of a current of uniform density. A greater effect is produced by an electrical current of a given strength when it is applied near the nerve centres than when it is applied to some part near the periphery, and it has been supposed that the wave of excitation as it travels downwards gathers strength like an avalanche, but this effect is only observed with electrical and not with chemical stimuli. Nerve tissue responds more readily to feeble currents of electricity than muscle, and some nerves, as for example those supplying the flexors of the leg in the frog, are more easily excited than others, as the extensors. The contact of a single pole of a battery, by disturbing the electric relation of the nerve, will produce contraction, which is then called "unipolar induced action."

Action of induced currents.—Induced or interrupted currents of electricity act very powerfully upon the nerves. The induced current which is established on *breaking* a current, has the same direction as this current, and is of very high tension. The induced current which is established on *making* contact is of feeble tension, is produced more slowly than the foregoing, and runs in the opposite direction. With equal strength of the inducing current, the

induced current which is established on breaking contact constitutes a much more powerful stimulus than that which is established on making contact. The maximum stimulus is always produced at the cathode, or negative pole. If induced currents are applied to a motor nerve, beginning with those of very feeble intensity, contraction first occurs with the induced current established on breaking contact. As the current increases in force, contraction occurs also on closing, so that with each interruption of the current two shocks are experienced, and by degrees, as the current is still increased in intensity, the two shocks tend to become equal in force.

Conditions of vitality of the nerves and grey matter.—These have been well given by Nuel, who observes that in the first place the nerves are remarkably independent of the circulation. A small nerve of a mammal will continue to react on stimulation for several hours, even when isolated from the adjoining tissues, and without any circulation of blood, providing that it is preserved from desiccation, and that circulation still continues in the proximal extremity of an afferent and in the distal extremity of an efferent nerve. The nerves, therefore, are very resistent of change; the grey matter of the nervous system is, however, very much more susceptible, since the cessation of the circulation for a minute or two abolishes its functions. Syncope can be almost instantaneously produced by simultaneous ligation or compression of the two common carotids and the two vertebrals, and temporary loss of vision can easily be induced by pressure on the globe of the eye. If a motor nerve of a mammal, with its muscle, be separated from the body, and its temperature is maintained whilst its desiccation is prevented, contraction of the muscle occurs on stimulation of the nerve for about half an hour, and when this has ceased the muscles will still respond to

direct stimulation, which is a proof that the loss of indirect excitability is not due to the condition of the muscle. After a time, however, the muscle ceases to respond to direct stimulation, though the nerve is still capable of conducting impulses, and presents the electrical manifestations characteristic of its vitality. It would appear, then, that in such a preparation the terminal plate first dies, then the muscle, and finally the nerve. It is remarkable that, from some as yet unexplained cause, before the indirect excitability of the muscle disappears, it augments very perceptibly, at first upwards towards the cut extremity of the nerve, and then downwards towards the periphery.

Necessity for continuity of tissue.—In order that a nerve should act as a conductor of nerve impulses it must be in direct continuity with its centre. If a nerve be divided, the centres can no longer act upon muscles through it, nor can any sensation be conducted by it from the periphery to the nerve centre. Within a week after division, "traumatic degeneration" begins in the peripheric extremity, the nerve becoming softer, its axis cylinder and medullary sheath breaking up into a fatty substance that appears in the form of drops, and an albuminous portion, the former of which, after a time, undergoes absorption.

The central ends of cut nerves do not degenerate, except as far as to the first node of Ranvier, for some considerable time after the section has been made; and it has been observed that if a posterior root of a spinal nerve be divided, that portion which is continuous with the ganglion does not degenerate, whilst the other part does. That portion of the fibre, therefore, which is still continuous with a cell retains its vitality. The central ends of cut motor nerves do not degenerate, for they are continuous with the cells in

the anterior horns of the grey substance of the spinal cord. It has hence been supposed that the nerve cells exert a trophic influence over the nerve fibres, and that it is only when a fibre is severed from the nerve cell from which it arises that it degenerates.

If the two extremities of a divided nerve be placed in apposition, even when a considerable time has elapsed, they will cohere, and their function may be re-established; and it is found that in the regeneration of mixed nerves the sensory fibres first recover their function, and then those which conduct motor impulses; so, in cases of paralysis, the sensibility of the arm or leg returns long before the patient is capable of calling any of the muscles voluntarily into play.

Electric currents in nerve.—Just as in the case of muscle, so with perfectly fresh nerve as it exists in the living body it is doubtful whether any electrical current exists; but a few minutes after removal from the body, if one end of a wire be placed on the surface or natural longitudinal section of a nerve, whilst the other is applied to the cut surface or artificial transverse section of the same, and a galvanometer be introduced into the circuit, it can be shown that a strong current sets from the longitudinal to the transverse surface; the former must therefore be positive, as compared with the latter, which is negative; as a consequence there must be within the nerve a current in the opposite direction, setting, that is, from the transverse section to the longitudinal section; and it has been suggested that a reason for this may be that the cut surface, being exposed to the air, oxydises more rapidly than the longitudinal surface, which is protected by the sheath of the muscle, and being the seat of more active chemical changes, is therefore positive to the longitudinal section. Two points that are equally distant from the equator of the longitudinal section of the

nerve, or from the centre of the transverse section, give no current, but if at unequal distances, then the most remote is positive as regards the other. The electromotor power of a large nerve is equal to 0·02 of a Daniell's cell, of a large and strong muscle 0·05 to 0·08. It increases on moderate elevation of temperature.

Physiological rheoscope.—This is a preparation of a frog, in which the longitudinal and transverse sections of the gastrocnemius are connected by any moist conductor; as soon as the sciatic nerve of a frog, which is isolated, but still in connection with the lower leg, is placed on this, a contraction of its gastrocnemius follows, and the same occurs when the sciatic is raised.

Negative variation of the natural electric current of muscle.—If a muscle be thrown into tetanus, and the electric current be tested, it will be found that the natural current rapidly diminishes, and sinks to zero, or that it may be actually reversed, especially if the primary muscle current have been strong, and if the muscle contract energetically.

Ritter-Valli's law.—If a nerve be divided, or if the centre is destroyed, the nerve, beginning at the central end, is rendered more excitable throughout; its excitability then diminishes till it becomes totally extinct. In cases of divided nerves the loss of excitability takes place much more quickly in the part connected with the centre than in the peripheral portion.

Electrotonus.—If a constant current be made to traverse a portion of the length of either a motor or sensory nerve, not only the part between the poles or "intrapolar" area, but the rest of the nerve, both above and below, undergoes a change. The current is called a polarising current; the change is that the nerve is thrown into a condition termed electrotonus. The excitability of that portion of the nerve which is situated near the positive pole is lowered, whilst the

excitability of that portion which is near the negative pole is exalted. This change may be shown by the application of any stimulus to the parts in question. Thus, if an electric current be used, a weaker current is required to produce the same effect if applied in the neighbourhood of the negative as compared with that required near the positive pole. The condition of the nerve on both sides of the positive pole is termed anelectrotonus, and on both sides of the negative pole, cathelectrotonus. There is, with moderately strong constant currents, a neutral region in the intrapolar area at which the excitability of the nerve is neither increased nor diminished; with weak currents this indifferent point is nearer the anode or positive pole, with strong nearer the cathode or negative pole of the constant current. The nerve experiences a stimulus at the moment when a current is closed and at the moment when it is opened, that is, at the moment when electrotonus is established and when it disappears; on closure of the current, this stimulus occurs at the cathode alone, or at the moment when cathelectrotonus is established; on opening the current the stimulus occurs at the anode alone, or at the moment when anelectrotonus is established. Of these two stimuli, that caused by the establishment of cathelectrotonus acts more powerfully than that caused by the disappearance of anelectrotonus. The contraction of muscle resulting from closure and opening of the current transmitted through a nerve differs with the direction and the strength of the current. (1) Very weak currents, whether directed upwards or downwards, only produce *contraction* on *closure* of the current, for the disappearance of electrotonus is then so feeble a stimulus that the nerve scarcely reacts. With currents of medium strength contraction occurs both with the ascending and with the descending current on opening and on closure. Very strong descending

currents cause contraction only with closure of the current. The opening current fails because nearly the whole intrapolar area is rendered incapable of conduction. Very strong ascending currents present only contraction on opening, on the same ground.

The following table may perhaps serve to render the action of currents of varying intensity more manifest:

Law of Spasm or Contraction.

Strength of Current.	Ascending Current.	Descending Current.
Weak . .	Closure, contraction. Breaking, rest.	Closure, contraction. Breaking, rest.
Moderate . .	Closure, contraction. Breaking, contraction.	Closure, contraction. Breaking, contraction.
Strong . . .	Closure, rest. Breaking, contraction.	Closure, contraction. Breaking, rest.

The effects of stimuli on afferent nerves are difficult to investigate. The method adopted is to induce extreme reflex irritability by means of strychnia, in order that peripheral stimuli may readily induce tetanic muscular contractions. The same laws appear to hold good.

Functions of nerves.—The different nerves may be divided into definite groups, which have certain features in common, whilst they present minor differences. The chief groups are:

(1) The centrifugally conducting nerves, which include:

a. Motor nerves for the striated muscles.
b. Motor nerves for the smooth muscles.
c. Secretory
d. Trophic
e. Inhibitory
f. Vaso-dilator
} nerves.

(2) The centripetally conducting nerves, which include,

a. Nerves of common sensation.
b. Nerves of special sense.
c. Nerves ministering to reflex action, or excito-motor nerves.

(3) Intercentral fibres.

The functions of these nerves are determined by the terminal apparatus and special structures with which they are connected at their extremities. The effects observed, for example, when a motor nerve is stimulated, being due to its distribution to muscle and connection with a motor nerve cell; and of a nerve of common sensation, to its distribution to the skin at one end, and to a sensory nerve cell at the other. The intimate relation between nerve and muscle is shown by the fact that cells have been found, one part of which is sensory while the other is contractile.

Mode of determining the function of a nerve.—If a hitherto undescribed nerve were discovered in the body, its function would be determined by a consideration both of its anatomical origin and distribution and of its physiological characters. In regard to its anatomical disposition, it would be noticed whether it sprang from a tract giving origin to other known motor nerves, and from large ganglion cells, and whether it was distributed to muscle, gland, skin, or membrane, or whether it simply connected different parts of the nervous system together. In regard to its physiological characters, it would be subjected to experiment; the effects of stimulation at some part of its course would be observed; it would be divided, and the effects of division, both immediate and remote, would be noticed; the peripheric stump would be stimulated with electrical currents, or other stimuli, and the results of such

irritation carefully noted, whether muscle contracted, or gland secreted, or some change occurred in the structure or function of the organs to which it had been ascertained, by anatomical investigation, to be distributed; and, lastly, the proximal stump of the divided nerve would be similarly stimulated and the effects observed. The adoption of these measures has shown that the purposes fulfilled by nerves, or their *functions*, differ remarkably.

Sensory nerves.—These are divided into nerves of common sensation and nerves of special sense. The nerves of touch, or common sensation, issue from the spinal cord by the posterior roots of the spinal nerves, which, after a short course, have a ganglion upon them. Immediately below the ganglion, the sensory roots join with the anterior or motor roots, and the ordinary mixed nerves (that is, nerves containing both motor and sensory fibres) are formed. If traced into the spinal cord, many of the sensory fibres are seen to be connected with small ganglion cells in the posterior horns of the grey matter. When traced in a peripheral direction, the nerves of common sensation are found to terminate chiefly in the skin. The evidence on which the function of a nerve is determined to be sensory is, that if it be divided there is loss of sensation in the parts to which it is distributed: stimulation of the distal extremity is without effect; stimulation of the proximal end produces pain and reflex movements. The nerves of special sense, including those ministering to vision, hearing, taste, and touch, will be subsequently considered.

Motor nerves.—Motor nerves are those which are distributed to muscle, and incite it to contract. The motor nerves of the body generally spring from the spinal cord or its continuation upwards in the medulla oblongata and brain. They issue from the spinal cord by the anterior roots, which are connected

with large cells in the cord, and terminate by piercing the sarcolemma of the muscle fibres, and becoming continuous with the proper muscular substance. On section of any motor nerve, the muscles supplied by it cease to be under the influence of the will, or become paralysed. Stimulation of the proximal end of the divided nerve is without effect; stimulation of the distal end causes contraction of the muscle until degeneration of the nerve has taken place.

Recurrent sensibility.—It has been said that, after division of a motor nerve, stimulation of the proximal portion is without effect; that is to say, that it produces neither motion nor pain. But this is not strictly correct; for, if the *motor* root of one of the spinal nerves be divided, and a stimulus applied to the cut surface of the distal portion, some pain is felt. It is believed that this is due to recurrent fibres of the sensory root, which, after having joined the motor root, instead of going as usual to the periphery, revert to the spinal cord, and enter it by the motor root. It has even been shown that the peripheral mixed nerves have some degree of recurrent sensibility. Thus, if the median nerve be divided, it is found that, after a few hours, the distal stump possesses sensibility. The sensory fibres, therefore, which run in the median nerve cannot all terminate in the periphery, but some of them must turn back and run in a recurrent direction in the ulnar or musculo-spiral nerves.

Secretory nerves.—This term is applied to those nerves which, when stimulated, excite secretion. The best-known examples are those of the chorda tympani, which, when stimulated, causes a flow of saliva from the submaxillary and sublingual glands; the nervus petrosus superficialis minor, which is a branch of the glosso-pharyngeal, and, after entering the otic ganglion, joins the auriculo-temporal nerve, and is

distributed to the parotid gland; when stimulated, it excites the parotid to secrete saliva; the lachrymal and subcutaneus malæ, which, when stimulated, cause a flow of tears; the nerves exciting the sweat-glands to secrete; and those distributed to the mammary gland.

Trophic nerves.—The belief in the existence of trophic nerves, or nerves ministering to the nutrition of a part, has been chiefly derived from observation of the effects of lesion of nerves. Thus, if the fifth nerve be divided in the skull, it is found that, after six or eight days, inflammation of the cornea sets in, and the whole eye, becoming gradually involved, is lost; and it is supposed that, the influence of the nerves having been removed by the section, the nutrition of the tissues is interfered with, and they die. But it has been pointed out that another explanation may be given of the phenomena, and that whereas in healthy conditions the surface of the eye is acutely sensitive, and the contact of foreign bodies is prevented by movements of the head, closure of the lids, and flow of tears; after section of the fifth nerve the sensibility is entirely lost, and particles of dust, organic ferments, and germs of various kinds, may easily adhere to the surface, whilst, no sensation of dryness being conducted to the reflex centres of the seventh nerve, the lids are not duly closed when required, and the cornea desiccates. In proof of this, it is asserted, first, that similar changes, though of a less serious character because the vaso-motor nerves are not implicated, may be observed when, from paralysis of the seventh nerve, the lids are kept permanently open; and secondly, that, if the cornea be preserved from the injurious action of foreign bodies by luting a watch-glass over the eye, the inflammatory symptoms may be prevented from occurring, and cured if they have commenced.

Inhibitory nerves.—This term is applied to nerves which arrest or prevent action. The brain exerts an inhibitory power over reflex actions in general. Thus, it is natural to start, or move the body or limbs, from any sudden stimulus, as a cut or burn; but the will can overpower this movement, and maintain the limb in position notwithstanding the pain. The best examples of inhibition are the action of the vagus nerve on the heart and the action of the splanchnics on the movements of the intestine. When the vagus is stimulated, the heart stops in diastole. The mode in which inhibitory impulses act is not clearly understood; but it may be conceived that impulses coming from one centre counteract or suppress those which are about to be liberated from another, just as two beams of polarised light of equal intensity, when meeting under a certain angle, occasion darkness.

Vaso-dilator nerves.—The best examples of these are seen in the nerves distributed to glands and to the erectile organs. In the case of the salivary glands, the blood, when the gland is at rest, flows from an opened vein slowly and with its usual dark colour; but when the nerves containing the vaso-dilating fibres are stimulated, the arteries distributed to the gland enlarge, and the resistance to the passage of blood through the gland falls so remarkably that the speed of the venous current is greatly augmented, and presents arterial pulsation, whilst the colour of the venous blood is as bright as that contained in the arteries. This change in the activity of the circulation is not necessarily accompanied by increased secretion. Similar phenomena may be seen in the erectile organs, but it is not known how the dilatation is effected.

Vaso-motor nerves.—These fibres might with propriety be termed vaso-constrictor fibres. They have for their function the contraction of the smaller

arteries. The vaso-motor fibres are chiefly contained in the sympathetic nerves, and, like the vaso-dilator nerves, have been particularly studied in the salivary glands and in the vessels of the ear. On stimulation of these fibres, the arteries contract, the supply of blood is greatly diminished, the veins return but little blood of a dark colour, and the temperature of the part falls; and in the case of the gland the secretion is checked and altered in quality. There is little doubt that each gland has its vaso-constrictor and its vaso-dilator fibres, but it is not practicable in most instances to isolate them.

Frey's experiments show that if the vaso-constrictor and the vaso-dilator fibres distributed to any organ be simultaneously stimulated, the action of the vaso-constrictor fibres predominates over that of the others; whilst, on the contrary, when the stimulation has ceased to be applied, the vaso-dilator fibres exert their action.

Rapidity of conduction in nerves.—The mode in which this has been determined consists, in the case of the frog, in isolating as long a portion as possible of the sciatic nerve, and applying a stimulus first to the end of the nerve most remote from the gastrocnemius, and then to the part which is nearest to the muscle, and obtaining simultaneous tracings with a rapidly-revolving cylinder, or with the pendulum myograph, of the moment when the current is applied, and of the contraction of the muscle. The rapidity with which impressions are conducted through *sensory nerves* has been given very differently by different observers, and even by the same observer experimenting on different persons. Thus Kohlrausch found the extremes of the rapidity of conduction of sensory impressions to be 56 and 225 meters per second. The mean of all his experiments gave 94 meters. De Jaager believed it to be 26 meters. The rapidity of conduction in *motor* nerves is about 34 meters per second in man. It is retarded by cold, and by the

condition of anelectrotonus, and in motor nerves by curare. It is augmented by warmth, by an increase in the strength of the stimulus, and by the establishment of cathelectrotonus. In man the contraction of the muscles of the thumb has been used for experimental purposes, the nerve-stimulus having been applied at one time to the median nerve in the axilla, and at another to the same nerve at the wrist. When a stimulus is transmitted through a nerve, it is found that the part of the nerve through which it is made to pass exercises considerable influence on the rapidity of conduction. This was first shown by Munk, who stimulated the motor nerve of a frog in three places, and found that with equal length of nerve the portion between the middle and lower points of stimulation conducted twice as rapidly as that between the upper and middle point.

Conduction in both directions.—It may be taken as certain that when either a nerve of common sensation or a motor-nerve is stimulated, the stimulus is propagated in both directions; so that a wave travels not only downwards in a motor and upwards in a sensory nerve, but upwards in a motor and downwards in a sensory nerve. The nerves are, in fact, only conductors, and the effect produced when they are stimulated depends upon the nature of the organ with which they are connected at their termination. Thus, if the hypoglossal and lingualis nerves, where they are in close contiguity to each other, be divided, and the peripheric extremity of the hypoglossus be united by a suture with the central end of the lingualis, when union has taken place, contractions of the muscles of the tongue can be produced by stimulation of the lingualis. The stimulus must here be propagated in the opposite direction to that which is natural in the sensory lingual nerve. Similar evidence has been obtained by Bert, who implanted

the abraded end of the tail of a rat into a cut in the skin of the back, and when it had become thoroughly adherent, divided the tail at its root. It was then found that sensory impressions were propagated along the tail in the reverse direction to that which they pursued previously to the section. The phenomena of electrotonus also show that the nerve is altered throughout its whole length by the application of a stimulus to any part of it.

Automatic movements.—This term is applied to movements which take place in response to stimuli generated in the nerve centres themselves, or which occur after removal of the whole of the nervous system, with the exception of that part from which the motor nerve springs. The best examples of it are the following: (1) Those of the continuance of the respiratory movements after the brain has been gradually removed from above and the spinal cord from below, until only a small portion of the medulla oblongata is left, giving origin to the phrenic and intercostal nerves. It is supposed in this case that the absence of oxygen, and the presence of carbonic acid gas in excess in the blood circulating through the medulla oblongata, stimulate the cells forming the respiratory centre, and that these automatically originate the movements observed.

(2) Those of the heart, in which rhythmical contractions occur after the organ has been entirely removed from the body, and therefore when no action of the central nervous system can take place. It is supposed in this case to be due to the rhythmical liberation of impulses from the ganglia situated in the heart itself.

(3) Those of the stomach and intestines, where, after isolation of a segment of the canal, peristaltic movements may still be observed, apparently without the application of any stimulus.

(4) Those of the uterus and of the bladder and

ureters, which move after the whole of the nerves distributed to them have been divided.

(5) Those of the iris, which has been seen to contract and dilate in some animals even after the anterior half of the eye has been removed from the body.

(6) Those of the arteries and of the lymphatic hearts, which have been observed in some animals to present contractile movements after destruction of the brain and spinal cord.

(7) Certain secretions, as those of the saliva and bile, which continue to be formed when all the nerves supplying the glands have been divided.

Reflex acts.—This term is applied to movements or secretory processes, which take place in response to a stimulus applied to some part of the nervous system. The conditions which are requisite are: (1) A stimulus, (2) afferent or centripetal nerves, (3) a nerve centre, (4) efferent or centrifugal nerves, (5) muscles or glands.

The stimulus may be one of the various kinds already mentioned, mechanical, chemical, thermic, or electric; or it may be of a special kind, as in the case of odorous or luminous stimuli. It may be applied either to the peripheric extremity of the nerves, which are in almost every instance connected with a special terminal apparatus, or to the nerves in some part of their course; the spinal reflex movements are, however, much more orderly and purposive, as well as swifter, in the former than in the latter case. The stimulus may also be applied to one of the special nerves, and act through the brain, as in the vomiting produced by a disagreeable sight or smell.

The distinction between a purely voluntary and a reflex act is in general sufficiently evident. The act of writing is a voluntary one; the formation of each letter is slowly learned, and even in those most

accustomed to write the process requires a distinct mental effort; but the act by which food is propelled down the œsophagus is a reflex act, and is performed quite independently of the will. In many instances reflex acts are performed with consciousness, in many without. The movements of the intestinal canal, of the gall-bladder, of the arteries, of the ducts of many glands are unattended by consciousness, whilst such reflex acts as coughing, sneezing, and winking of the eyelids are clearly perceived. In some instances, as in contraction of the pupil, the stimulus may be clearly perceived; but the contraction of the muscular tissue of the iris is wholly without consciousness.

The vivacity and energy of reflex acts bears no relation to the amount of pain produced. Thus, if an eel be decapitated, and the surface of the body be lightly touched, strong reflex movements are produced; but if a thermocautery be applied to the skin, a severe burn may be inflicted with very slight muscular contractions. In man, in the same way, tickling will produce more vigorous movements than a blow. A stimulus which is so feeble as not to excite a reflex act may by repetition induce it.

Laws of reflex action.—Reflex actions are not irregular, but respond in a very definite manner to particular stimuli, and certain laws have been discovered to exist, the more important of which are the following:—

(1) *Law of unilateral action.*—If the skin or other sensory surface be stimulated, the muscles of the same side or of the immediate vicinity are stimulated to contract. If the skin of one leg be stimulated, that leg will be drawn up by its muscles. If one conjunctiva be touched, the lids of that side close.

(2) *Law of irradiation.*—If the stimulus be stronger than that required to produce unilateral action,

the next effect is that the corresponding muscles of the opposite side are made to contract. This is sometimes called the law of reflex symmetry. If the stimulus be still stronger, it affects not only the muscles of the opposite side, but those muscles which are supplied by nerves arising higher up from the spinal coad. The muscles supplied by lower nerves are rarely affected.

(3) *Law of co-ordination.*—This, which might also be termed the law of purposive adaptation, indicates that the movements made in response to a definite stimulus are not irregular, but are performed with a distinct object, and are co-ordinated to that end. Thus, if a frog be decapitated, and the body be suspended by the fore-limbs, if the side of the abdomen be touched with a feather dipped in acetic acid, the leg of that side is raised, and the foot is so moved as to brush away the stimulus ; and if this leg be held down, the opposite foot will be raised, and after being made to cross the back will attempt to perform the same movement.

(4) *Law of prolonged irritation.*—This law shows that a powerful stimulus produces a persistent action on the spinal cord. Thus, if the head of a frog be violently struck against a hard body, the animal is thrown into a tetanic state, and this tetanic condition is maintained even after decapitation.

Rapidity of reflex acts.—The rapidity with which a reflex act is performed has been determined to vary, according to the intensity of the stimulus, between 0·025 and 0·05 second. The time occupied between contact with the cornea and contraction of the orbicularis palpebrarum is 0·05 second. Cold lowers the rapidity of reflex acts. Chloroform retards them. The administration of strychnia accelerates them. Moderately high temperature accelerates them.

Some reflex acts are of so complex and purposive a character as almost to suggest a certain degree

of consciousness in the spinal cord, since they take place after the brain has been removed; such are the crawling movements of a frog when the board on which it lies is tilted, and the fluttering of the wings of birds. A remarkable experiment is known as "Goltz' Quarrversuch," in which a frog, from which the brain has been removed, is made to croak by stroking the skin of the back.

Functions of the cerebral nerves.—The cerebral nerves are twelve in number, and their functions may here be briefly given:—

(1) *The olfactory nerve.*—The olfactory nerve arises from the olfactory bulb, which is really a process of the brain itself, and whilst small and degenerate in man, is large and highly developed in many animals, with extensive intracerebral relations. It is distributed to a definite region of the nose, the epithelium of which presents special characters. (*See* Klein's "Histology.") Stimulation of this nerve by its proper stimuli excites odorous sensations. It reacts but slightly, if at all, to mechanical or other stimuli. Its division or non-development is attended with absence of the sense of smell. For the sense of smell to act it is necessary that the membrane should be moist, and that the stimulus should be in the gaseous state, or at least in a state of such fine division as to be suspended in the air. In consequence of the distribution of the fifth nerve to part of the Schneiderian mucous membrane, pain or tingling may be experienced with certain odorous substances, such as ammonia or carbonic acid gas.

(2) *Optic nerve.*—The optic nerve and tract conduct visual impressions from the retina to the brain. The optic tract arises chiefly from the grey matter of the optic thalamus, and from the corpora quadrigemina, but other fibres may be traced into the medulla oblongata and spinal cord, and others again radiate towards

the apex of the occipital lobe of the cerebrum, where, according to some authors, the psychic centre of the visual sense is located. The terminal apparatus of the optic nerve in the eye is the retina. The normal stimulus of the optic nerve is light, but luminous sensations can be excited by other stimuli, as by pressure, concussion, and electricity. Various reflex acts can be induced through the optic nerve; thus light falling on the retina causes contraction of the iris by a reflex influence acting through the third nerve upon the sphincter pupillæ, whilst the absence of light acts through the sympathetic nerve in inducing dilatation of the pupil. Exposure to bright lights, again, causes closure of the lids by reflex impulses conveyed through the facial nerve; and, lastly, a flow of tears may be induced by reflex impulses conducted through the fifth nerve. Section or destruction of the nerve causes complete and permanent blindness.

Third or oculo-motor nerve.—The third nerve arises in common with the fourth from a nucleus situated just below the Aquæductus Sylvii, which is a continuation of the anterior horn of the grey substance of the spinal cord. It is in relation with the nates, and with the lenticular nucleus. It is connected in the cavernous sinus with the first branch of the fifth nerve, and thus obtains fibres ministering to muscular sensibility, and with the sympathetic nerve which supplies it with vaso-motor branches. It is distributed to the muscles rotating the globe of the eye, named the rectus superior, rectus internus, rectus inferior and the obliquus inferior, and also to the levator palpebræ superioris. It gives a branch in the orbit to the ganglion ciliare, which is named its short or motor root, and through this supplies two muscles within the eye, the sphincter pupillæ and the ciliary muscle or tensor choroideæ, by means of which the accommodation of the eye for near objects is effected. The three centres which usually act

together, viz. for accommodation, for contraction of the pupil, and for convergence of the eyes, accomplished by the recti interni, are situated in that order from before backward in the posterior part of the floor of the third ventricle. The centre for the reflex contraction of the pupil from light falling on the retina is situated in the medulla oblongata. Atropin, daturin, duboisin, and other drugs paralyse the intraocular fibres of the third. Calabar bean, opium, and others act as stimuli to them. Complete paralysis of the third nerve is followed by (1) dropping of the upper lid, termed ptosis, (2) immobility of the eye in all directions, (3) eversion of the eye or external squint owing to the unantagonised action of the external rectus, (4), slightly increased prominence of the eye owing to the action of the obliquus superior, (5) dilatation of the pupil, (6) immobility of the pupil on exposure of the eye to light, and (7) loss of the power of accommodation.

Fourth nerve, or trochlear nerve.—This is the smallest of the cerebral nerves, and supplies one muscle only, the superior oblique muscle of the eye. The fibres of origin spring by an anterior root from the trochlear nucleus, which is continuous with the anterior horn of the spinal cord, and is situate near the valve of Vieussens, and by a posterior root connected with the ganglion of the fifth. Stimulation of the nerve causes contraction of the superior oblique muscle, and the eye rolls downwards and outwards.

When paralysed there is double vision, becoming more and more marked as objects below the plane of the horizon and towards the median plane are looked at. The false visage is on the same side as the affected eye, oblique, inclined inwards above, and appears lower and somewhat nearer than that of the healthy eye.

Fifth nerve, or nervus trigeminus.—This nerve is the nerve of common sensation for the side of the head and face, and supplies the muscles of mastication with

motor fibres. It is named the trigeminal from its dividing into three large branches just beyond the Gasserian ganglion. It arises by two roots, which appear at the side of the pons; the anterior is the smaller, and is a motor nerve; the posterior is larger, and is sensory. The motor root springs from a grey mass near the middle line of the floor of the fourth ventricle. The sensory root springs from a grey nucleus situated in the pons, from the medulla oblongata, and from the grey substance of the posterior cornu of the spinal cord, as far down as the third or fourth cervical vertebra. The trophic root springs from a grey mass at the side of the Aquæductus Sylvii. Other fibres spring from the substantia ferruginosa, from the cerebral peduncle, and from the cerebellum. If the distribution of the nerve be followed in the order of the three divisions, the functions of the branches are as follow:—

First or ophthalmic branch.

(1) Recurrent branch supplies sensory branches to the tentorium cerebelli.
(2) Lachrymal nerve supplies secreto-motory branches to the lachrymal gland, sensory branches to the conjunctiva, upper lid, and temple.
(3) Frontal nerve supplies sensory branches to the brow and upper lid.
(4) Nasal nerve supplies sensory branches to the conjunctiva, caruncle and lacrimal sac, to the tip of the nose and part of the septum, and gives off the long or sensory root to the ciliary ganglion.

The second or superior maxillary nerve.

(1) Recurrent nerve supplies sensory branches to the dura mater.

(2) Subcutaneous malar supplies sensory branches to the cheek and temple, and some secreto-motor fibres to the lachrymal gland.

(3) Superior, posterior, and middle alveolar nerves supply the teeth and upper jaw with sensory fibres.

(4) Infraorbital nerve supplies the lower lid, cheek, ala of the nose, and upper lip with sensory branches.

The third or inferior maxillary nerve.

(1) Recurrent nerve supplies sensory branches to the dura mater.

(2) Pterygoid, temporal, masseteric nerves supply motor branches to the muscles of mastication.

(3) Buccinator nerve supplies sensory fibres to the buccal mucous membrane.

(4) Lingualis nerve supplies nerves of special sense to the tongue, anterior arches of the palate, tonsils, and floor of the mouth. It contains vasomotor and vasodilator nerves for the vessels of the tongue.

(5) Alveolar nerve supplies sensory fibres to the gums and skin of the chin and lower lip, and motor fibres to the mylo-hyoid, anterior belly of the digastric, triangularis menti and platysma muscles.

Four ganglia are connected with the branches of the fifth pair of nerves, the ciliary, sphenopalatine, submaxillary, and otic.

(1) The **ciliary or lachrymal ganglion.** — This is connected with the ophthalmic division of the fifth, lies in the orbit, and has three roots: a short *motor* root from the third, a long *sensory* root from the nasal nerve, and a *sympathetic* root from the carotid plexus.

It gives off *sensory* fibres to the cornea and conjunctiva, the iris, choroid, and sclera; *vaso-motor* fibres for the vessels of the iris, choroid, and retina; *motor* fibres for the dilatator of the pupil; and lastly, *trophic* nerves for the eye.

(2) The **spheno-palatine ganglion** is situated just below the second division of the fifth, where it traverses the spheno-maxillary fossa. It receives *sensory* fibres from the second division of the fifth; *motor* fibres from the facial, through the nervus petrosus superficialis major; and *sympathetic* fibres from the carotid plexus.

It gives off *sensory* fibres to the interior of the nose, hard and soft palate, and tonsils; *motor* fibres to the levator palati, and azygos uvulæ; *vasomotor* fibres to the mucous membrane of the nose; and probably *secretory* fibres to the glands of the Schneiderian mucous membrane.

(3) The **otic ganglion** is situated just below the foramen ovale on the inner side of the inferior maxillary nerve, close to the origin of the internal pterygoid branch. It receives *motor* fibres from the third division of the fifth; *vasomotor* fibres from the sympathetic plexus surrounding the arteria meningea media; and *sensory fibres* from the glosso-pharyngeal through the nervus superficialis minor.

It gives off *motor* fibres to the tensor tympani and to the tensor palati muscles; and *secretomotory* fibres to the parotid gland, which join the auriculo-temporal nerve.

(4) The **submaxillary ganglion,** or **plexus.** This is situated above the deep portion of the submaxillary gland. It receives *motor* fibres from the chorda tympani, and therefore from the facial nerve; *sensory* fibres from the third division of the fifth; *vaso-motor* fibres from the sympathetic plexus surrounding the facial artery. It gives off *vaso-dilator* fibres obtained

from the chorda tympani, causing dilatation of the vessels of the gland; *secretomotor* fibres through the same channel, stimulation of which excites the secretion of the submaxillary gland, and *trophic* fibres to the same gland.

The *sixth nerve*, or *abducens oculi*. — This nerve springs from a nucleus continuous with and above that of the facial nerve, and continuous also with the anterior horn of the grey substance of the spinal cord. It is situated at the upper part of the floor of the fourth ventricle. It appears at the posterior border of the pons. It is a motor nerve and supplies one muscle only, the external rectus. It contains some vasomotor fibres, and some fibres conferring upon it muscular sensibility, which are derived from the sympathetic and the fifth, from both of which it receives branches in the cavernus sinus.

The *seventh nerve*, or *portio dura*.—The portio dura is a motor nerve distributed to the muscles of expression and to the salivary glands. It arises from the facial nucleus, situated near the upper part of the floor of the fourth ventricle, and from the lenticular nucleus of the opposite side. It appears at the upper part of the medulla oblongata in a triangular space, bounded above by the pons, in front by the olivary and behind by the restiform body, and is here divided into two parts, the smaller of which is named the portio intermedia. This intermediate portion is a remnant of a condition present in the lower animals, in which the facial and glosso-pharyngeal nerve issue together as a mixed nerve. The fibres of the portio intermedia may be traced into the glosso-pharyngeal nucleus. It is supposed that they may contribute gustatory fibres and vascular nerves. The portio dura is distributed: (1) By the nervus petrosus superficialis major to the levator palati and azygos uvulæ, having previously entered the sphenopalatine ganglion.

(2) By branches passing through the otic ganglion to the tensor palati and tensor tympani. (3) It supplies the stapedius. (4) It gives off secreto-motor fibres and vaso-dilator fibres to the sublingual and submaxillary glands. (5) It contains some gustatory fibres, probably derived from the glosso-pharyngeal nerve at its origin. (6) It contains the sweat-gland nerve fibres of the face. Lastly, it supplies all the muscles of expression of the face, the stylo-hyoid, posterior belly of the digastric, and the muscles of the external ear. Section or lesion of this nerve causes facial paralysis. The lids cannot be closed, the face is without expression on the side of the injury, the mouth is drawn up to the opposite side, speech and smell are rendered imperfect, and the secretion of saliva is diminished.

The *eighth* or *auditory nerve*, or *portio mollis of the seventh.* — This nerve arises from two nuclei, situated in the floor of the fourth ventricle; some fibres spring from the grey substance of the spinal cord, and some extend into the cerebellum, and even into the cerebral peduncle and cerebrum. The auditory makes its appearance in close proximity to the facial, from which it is separated by the portio intermedia. The nerve fulfils two functions: it is the nerve of hearing, or that by which sound undulations are conducted from the labyrinth; and secondly, by the distribution of some of its fibres to the semicircular canals and ampullæ, it aids in the preservation of the upright and normal position of the body, or affords the information by which the equipoise of the body is maintained. Division of the nerve causes permanent deafness; stimulation of it, auditory sensations. Section of the semicircular canals leads to vertigo and pendulum-like movement of the head.

Ninth or *glosso-pharyngeal nerve.*—The glosso-pharyngeal nerve is partly motor, partly sensory, and partly a nerve of special sense. It arises from a

nucleus situated in the lower half of the floor of the fourth ventricle, consisting partly of small cells, from which the sensory and special sense fibres arise, and partly of large cells; some fibres also arise from the spinal cord. The *motor* fibres are distributed to the stylo-pharyngeus, the middle constrictor of the pharynx, and perhaps also to the palato-glossus, levator palati, and azygos uvulæ, but these branches may be derived from the facial by the communicating branch between this nerve and the petrosal ganglion of the glosso-pharyngeal.

The *sensory* fibres supply the posterior part of the tongue, the anterior surface of the epiglottis, the tonsils, the anterior pillars of the fauces, the soft palate, and part of the pharynx.

The *special sense* fibres which minister to the sense of taste are distributed to the posterior third of the tongue, the sides of the soft palate, and the pillars of the fauces.

Tenth nerve, vagus or *pneumogastric nerve.*—This nerve has the widest distribution of any nerve in the body. It supplies the larynx and pharynx, the heart and lungs, the stomach, intestines, and liver, spleen, pancreas, kidneys, and bladder. It arises from a nucleus in the lower part of the floor of the fourth ventricle, and appears at the side of the medulla oblongata, in front of the restiform body and just below the glosso-pharyngeal nerve. The names, distribution, and functions of the chief branches which it gives off are :

(1) The meningeal branch, distributed to the meningeal artery, and to the occipital and transverse sinuses. The fibres are sensory.

(2) The auricular branch, distributed to the meatus auditorius, sensory in function.

(3) Connecting branches, the function of which is unknown, between the ganglion petrosum of the

glosso-pharyngeal and the ganglion jugulare of the vagus. A large communicating branch enters the vagus from the spinal accessory nerve, just below its lower or plexiform ganglion. This contains the fibres, which, after coursing in the trunk of the nerve for some distance, leave it, to be distributed as motor nerves to the muscles of the larynx and œsophagus, and as inhibitory nerves to the heart.

(4) The superior laryngeal nerve gives off sensory fibres to the mucous membrane of the larynx, the stimulation of which induces coughing by reflex action through a centre situated on each side of the raphe, near the ala cinerea. It supplies, in addition, motor fibres to the crico-thyroid.

The inferior laryngeal nerve supplies motor fibres to the trachea and œsophagus, and to the various muscles of the larynx. Section or lesion of the superior laryngeal nerve is apt to cause death by the entrance of food into the air passages, which are no longer protected by the natural exquisite sensibility of the laryngeal mucous membrane. Section or lesion of the inferior laryngeal nerve alters the voice, and is apt to cause death on slight exertion, owing to suffocation from the falling together of the vocal cords.

(5) The depressor nerve, given off from the superior laryngeal nerve and the trunk of the vagus in the rabbit, and passing into the cardiac plexus. It conducts impressions centripetally, and lowers the energy of the vaso-motor centre, causing the blood pressure to sink, and the heart to beat more frequently but less vigorously.

(6) The vagus gives off cardiac branches, some of which contain sensory fibres, others inhibitory fibres, and some accelerating fibres.

(7) The pulmonary branches of the vagus are partly motor, supplying the muscular fibres of the bronchi; partly vaso-motor, the fibres being derived

from the sympathetic; and partly sensory, some of the latter conduct impulses from the mucous membrane, which excite the cough-centre, whilst others excite the respiratory centre.

(8) The branches distributed to the œsophagus, stomach, and intestines are partly motor and partly sensory.

Landois observes that the trunk and branches of the vagus contain various *centripetal* fibres, which act on certain nervous mechanisms. These are:

(1) Fibres acting on the *vaso-motor centre*, some of which are *pressor* fibres, chiefly contained in the laryngeal nerves, which act in a reflex manner, and cause the arteries to contract, the blood pressure consequently to rise, and the heart to beat more frequently. Others are *depressor* fibres, which have an opposite effect.

(2) Fibres acting on the *respiratory centre*, some of which excite the centres and accelerate the respiratory acts, whilst others, situated in the two laryngeal nerves, depress and inhibit them.

(3) Fibres acting on the cardiac inhibitory centre, which run to this centre, and excite it to action. The existence of these is shown by stimulation of the proximal end of one divided vagus, which arrests the heart in diastole through the opposite one. Blows or sudden distension of the stomach produce the same effect.

(4) Fibres acting on the vomiting centre, which can be excited by stimulation of the proximal end of the divided vagus.

(5) Fibres which, when stimulated, induce arrest of the pancreatic secretion, and run centripetally, since this also may be induced by stimulation of the proximal cut extremity.

(6) Lastly, fibres may be shown by the same means to exist, which act in a reflex manner in inducing the formation of sugar in the liver.

Eleventh or *spinal accessory nerve.*—This nerve springs by one fasciculus from the accessory nucleus of the medulla oblongata, which is in near relation with the nucleus of the vagus, and by another fasciculus from a nucleus which extends down the spinal cord, between the anterior and posterior roots of the spinal nerves, as far as to the fifth or sixth cervical vertebra. This portion, which confers its specific name on the nerve, joins the vagus, and contributes to that nerve the inhibitory nerve-fibres it gives off to the heart, as well as its motor fibres to the larynx. The accessory nerve terminates in the sterno-mastoid and trapezius muscles, and it also contains some fibres of muscular sensibility, derived from the posterior roots of the first and second cervical nerves. The evidence demonstrating that the spinal accessory nerves contain cardiac inhibitory fibres is, that if the lower roots be divided, the fibres of the vagus going to the heart cease to exert an inhibitory action upon that organ; and, further, that these fibres undergo fatty degeneration.

Twelfth or *hypoglossal nerve.*—This nerve arises from two nuclei with large cells, and one nucleus with small cells, situated near the point of the calamus scriptorius. Some fibres also proceed from the brain, and from the olivary body. The apparent origin is from the side of the medulla oblongata, on a line with the anterior roots of the spinal nerves. The hypoglossal nerve is the motor nerve of the tongue, and supplies all the muscles by which it is moved, including the genio-hyoid and thyro-hyoid. It contains vaso-motor nerves for the vessels of the tongue, which it receives from its connection with the superior cervical ganglion. It further receives branches from the ganglion of the trunk of the vagus, and a small branch from the lingual of the fifth, by which it acquires the power of conducting impressions of muscular

sensibility. From its loops of communication with the upper cervical nerves branches are given off to the sterno-hyoid, sterno-thyroid, and omo-hyoid. Section of the hypoglossal nerves in man abolishes the power of movement of the tongue, and therefore interferes with mastication, deglutition, and speech.

The Sympathetic System of Nerves.

This consists of a series of ganglia arranged on either side of the vertebral column, connected by cords with each other, and also with the spinal cord, and of numerous scattered ganglia, from which branches are given off, chiefly to the organs of vegetative life, as to the alimentary canal and its appendages, the blood-vessels, and generative system. The nerves respond to the same stimuli as those belonging to the cerebro-spinal system.

Cervical portion of the sympathetic.—This consists of three well-known ganglia, and their connecting cords, and the influence of this part of the sympathetic has been chiefly ascertained by observing the effects of section and of stimulation. The effects of section are for the most part attributable to dilatation of the smaller arteries, increased blood-pressure, and the passage of a freer current of blood through them. Such hyperæmia, for example, affecting the retina renders it more sensitive to light; the pupil, therefore, contracts; the eye in the rabbit is drawn inwards; the lids are partially closed; the membrana nictitans is drawn over the eye; the secretion of tears is augmented; the sensibility becomes more acute. The temperature is notably heightened; the secretions of cerumen and of sweat are increased; a galvanic current too weak to act on the other side may here produce contractions. When the animal is killed the reflex faculty lasts longer there than on the

other side; cadaveric rigidity comes on later and lasts longer; putrefaction supervenes later; lastly, certain trophic disturbances occur chiefly in the region of the eye. On the other hand, on stimulation of the nerve the opposite effects are observed, such as dilatation of the pupil, diminished temperature, and contraction of the blood-vessels. There appear then to be in this part of the sympathetic pupil-dilating fibres, motor fibres for Müller's smooth muscle of the orbit, vaso-motor branches, secretory and trophic fibres. Besides these, the cervical sympathetic seems to contain branches which join the automatic ganglia.

Thoracic portion of the sympathetic.—The chief nerves emanating from these ganglia, which are about twelve in number, join the solar plexus and semilunar ganglia, and contain accelerating fibres for the heart, which, when stimulated, act centripetally on the inhibitory cardiac centre in the medulla oblongata; also fibres which excite the vascular nerve centres in the medulla oblongata; and lastly, the splanchnics, which act as inhibitory nerves on the movements of the intestine so long as a normal current of oxydised blood traverses the vessels, but if the blood has become venous the movements are intensified. The splanchnics are also the chief vaso-motor nerves of the vessels supplying the abdominal viscera. When the splanchnics are divided an immense accumulation of blood takes place in the abdominal vessels. The thoracic portion also contains inhibitory fibres for the renal secretion; fibres, stimulation of which causes sugar to appear in the urine.

Abdominal and lower parts of the sympathetic.—The nerves which are given off from the abdominal and lumbar ganglia chiefly enter into the plexuses which surround the vessels passing to the genito-urinary apparatus, and, so far as is known, are chiefly vaso-motor in function.

Functions of the Spinal Cord.

The cord is a centre for many reflex actions. It is a conductor between the brain and the various tissues and organs of the body. In man it is incapable of automatic action, and is destitute of consciousness, but in many of the lower animals there is reason to believe that it participates with the brain in these functions. (For details of structure see Klein's "Histology," p. 127, *et seq.*)

The spinal cord gives origin to thirty-one pairs of nerves, which are divided into groups in accordance with the part of the cord from which they spring, and are named respectively cervical, dorsar, lumbar, sacral, and coccygeal. Each nerve springs by two roots, an *anterior* and a *posterior*. Experiments devised by Sir Charles Bell and by Magendie have demonstrated that the *posterior* roots are *sensory* in function, and that the *anterior* are *motor;* and the general characters of these nerves have been already described (page 315). The evidence on which the function of these roots has been determined is that when the *posterior* root is touched or cut acute pain is experienced, and simultaneous reflex muscular contractions occur; when cut, the parts supplied by the nerve beyond the point of section are deprived of sensation. Stimulation of the distal stump when the nerve has been divided has no effect; stimulation of the proximal stump produces pain and reflex actions.

When the *anterior* root is divided contraction occurs in the muscles supplied by the nerve owing to the mechanical irritation of the knife, and some pain is experienced owing to recurrent sensibility. The muscles supplied by it are paralysed. Stimulation of the peripheric stump causes muscular contractions in the muscles supplied by the nerve. Stimulation of the proximal extremity is without effect. The

common sensation of the parts supplied by the nerve is not interfered with.

Functions of the intervertebral ganglia.—The functions of the ganglia on the posterior roots of the spinal nerves, and of the isolated ganglion cells found in these roots, have only lately been studied with care. Waller, in 1852, and Schiff more recently, showed that after section of the posterior roots between the spinal cord and the ganglion, the central portion of the root underwent degeneration, whilst the distal portion, which was still in connection with the ganglion, preserved its normal histological characters. When the motor root was divided they found that the distal stump alone degenerated. They therefore drew the conclusion that the intervertebral ganglia acted as trophic centres for the sensory fibres of the spinal nerves and posterior roots. The subject has again been worked at by Bechterew and Rosenbach. These observers divided the long roots forming the cauda equina in the dog, and noted appearances which corroborated Waller's statement. The axis cylinders in the central stump of the divided posterior roots had in many fibres disappeared, and in others were atrophic; the medullary substance was abnormally yellow, and frequently presented a granular aspect and an irregular contour. The connective tissue trabeculæ were abnormally thick, the blood-vessels filled with blood corpuscles. The distal segment of the cut posterior roots was healthy. Careful examination of the cord demonstrated that the nerve cells in both the anterior and posterior cornua for some considerable distance up the cord had, to a large extent, atrophied, and their place was occupied with spaces partially filled with their granular remains. Degeneration of many of the fibres of the continuation of the posterior roots in the grey substances of the cord was also observed, especially in those fibres which

ascend in front of the substantia gelatinosa Rolandi. In regard to the white columns of the cord, regeneration was well marked in the whole of the posterior columns near the lumbar enlargement, but higher up it was limited to the posterior median, or Goll's column, and especially to its innermost portion. The other columns were little affected, though a few fibres of the cerebellar column were degenerated. We may hence conclude that the ganglia and cells in question exert a trophic influence, both on the sensory fibres and roots of the spinal nerves, and also upon the ganglionic cell elements in the cord itself. There is a strong disposition to specialisation of function in different parts of the nervous system, so that besides afferent nerves ministering to ordinary sensation, and motor nerves to striated muscle, the spinal nerves contain sensory nerves of various kinds, such, for example, as those of tactile sensibility, pain, temperature, and tickling and motor fibres which are distributed to the smooth muscular tissue of various organs, as the uterus, urinary bladder, and blood-vessels, and there are in addition efferent, secreto-motor, and trophic fibres.

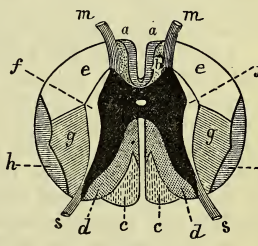


Fig. 15.

The black part in the centre of the figure is the grey substance; *m*, motor anterior root; *s*, posterior sensory root; *a* and *g*, pyramidal columns; *b*, fundamental fasciculus of the anterior column; *c*, Goll's column; *d*, Burdach's column; *e* and *f*, mixed lateral columns; *h*, cerebellar columns.

The course of these fibres after their entrance into the cord is not very accurately known; but there seems to be good reason for believing that the cord, besides its apparent division into grey and white substances, may be mapped out into certain columns formed

by ascending or descending groups of fibres, which are represented in the accompanying woodcut (Fig. 15), made transversely across the spinal cord at the level of the third dorsal vertebra.

The **grey substance of the cord.**—This is essentially composed of cells and their processes, and although it may be regarded as a series of centres which respond readily to appropriate stimuli, it is certain that it is quite unexcitable to direct irritation, such as cuts, punctures, or electric stimuli. The cells are roughly divisible into two groups: those situated in the anterior cornu, which are large, and appear to be capable of liberating motor impulses; and smaller cells, situated in the posterior, which receive and transmit sensory impressions.

Schiff has been led, from his experiments, to admit that whilst motor impulses and impressions of touch, temperature, and muscular sensibility travel along fibres situated in the white columns of the cord, those for the conduction of pain run in the grey matter, for section of the whole of the white columns abolishes the power of perceiving tactile sensations and of temperature and muscular sense; pain is still felt, whilst if the grey matter be destroyed the sense of pain is lost, whilst the others are, though more or less impaired, preserved.

The **white substance of the cord.**—This is composed of fibres, and surrounds the grey substance. It is divisible into several columns or groups of fibres, which have received special names.

Of the several groups of fibres differentiated in Fig. 15, the columns marked *a* and *g* contain all fibres emanating from the central convolutions of the cerebral cortex and conducting voluntary impulses, or impulses to muscles under the control of the will. The decussation of the pyramids at the lower part of the medulla oblongata is formed by the decussation of

these fibres, and, before they emerge from the cord by the anterior roots, they enter the grey substance of the cord.

The column *h* is composed of fibres connecting the cerebellum with the grey substance of the spinal cord. *b*, *e*, and *f* are the columns connecting the reflex centres situated in the grey substance of the cord and medulla oblongata, and they also contain those fibres which are continuous with the anterior roots of the spinal nerves, and which subsequently enter the grey substance. *c* is a column composed of fibres connecting the posterior roots with the grey nuclei of the funiculi graciles of the medulla oblongata; *d* is composed of fibres connecting the posterior roots and the grey substance of the cord and medulla oblongata (Landois).

Course of the fibres of the anterior and posterior roots of the spinal nerves.—If the *anterior* roots of the spinal nerves be followed after their entrance into the cord, they appear for the most part to join the large ganglion cells of the anterior cornu of the grey substance, of which they form the axis-cylinder processes. From the grey fibrous plexus which these ganglion cells give off, broader fibres take origin. Some of these, constituting the median fasciculus, pass through the anterior white commissure to the opposite side, and ascend in the anterior column of the latter. Others, constituting the lateral fasciculus, enter the lateral column of the same side, and ascend until they decussate at the lower part of the medulla oblongata, forming the decussation of the anterior pyramids.

On entering the medulla oblongata the motor fibres of the cord ascend as compact columns, which may be followed to the deep surface of the olivary bodies and corpora quadrigemina, forming the pyramidal tract of the encephalic isthmus of Flechsig, whilst some emerge as arcuate fibres, and pass to the cerebellum; travelling through the pons the motor

tracts enter the crura cerebri and constitute the larger part of the crusta of each cerebral peduncle; from thence they enter the internal capsule and diverge in the corona radiata, to reach the cortex cerebri; some probably becoming connected with the ganglion cells forming the great ganglia at the base of the brain.

As soon as the *posterior roots* arrive at the spinal cord, these fibres, after losing their sheath, pass partly into the posterior grey cornu and partly into the posterior lateral, posterior median, and direct cerebellar columns of white substance in which they ascend the cord; of the fibres entering the posterior grey cornu, some terminate in the small ganglion cells of this region, others run towards the anterior cornu, but the majority appear to cross the median line, and to enter the grey substance of the opposite side of the cord. In the medulla oblongata it is found that the fibres of the posterior median, or Goll's column, form the greater part of the *funiculus gracilis*, and end in part of the cells of the nucleus gracilis. The fibres of the posterior lateral, or Burdach's column, enter the *funiculus cuneatus*, and its nucleus. The fibres of the direct cerebellar column form the *corpus restiforme*, and pass to the cortex and central grey substance of the vermiform process of the cerebellum. Many sensory fibres ascend through the formatio reticularis of the medulla oblongata. In the pons the sensory tracts lie in the formatio reticularis and lemniscus. In the crus cerebri they occupy the tegmentum lying external to the red nucleus. Finally, coursing along the inner half of the posterior third of the internal capsule they probably enter in part into the corona radiata, and run directly to the parietal region of the cortex cerebri, and in part to the medullary laminæ of the optic thalamus, whilst some terminate in the substantia nigra of the crus cerebri.

Course pursued by sensory impressions and motor impulses through the cord.—Tactile sensations, such as those of temperature, pressure, and muscular sensibility, travel through the posterior roots of the spinal nerves into the posterior cornu, then after decussation along the lateral column of the opposite side; painful impressions also enter through the posterior roots, and travel upwards in the lateral columns of the opposite side, but they also appear to be capable of conduction through the grey substance generally. Motor impulses travel in the upper part of the cord along the anterior and lateral columns, in the lower part along the lateral columns alone. Reflex centres are probably connected by fibres running in the white anterior and posterior columns. Inhibitory fibres, controlling reflex acts, travel in the anterior columns. The vaso-motor nerves run in the lateral columns, and issue with the anterior roots of the spinal nerve.

Effects of the section of the cord.—If one lateral half of the spinal cord be divided in the middle of the dorsal region, the effects observed are what might be anticipated from what has just been stated in regard to the course of the fibres in the cord; for since the sensory fibres of the posterior roots for the most part decussate immediately and pass up the other side of the cord, whilst the motor fibres of the motor roots run vertically on their own side till they reach the medulla, such lesion will cause paralysis of motion in the muscles of the same side below the plane of the section, and paralysis of sensation in the skin and other parts of the opposite side. Vaso-motor paralysis, indicated by enlargement of the vessels, increased temperature and hyperæsthesia, takes place on the side of the lesion. If a section be made of the whole length of the cord commencing below the decussation of the pyramids and proceeding downward so as to divide it into two lateral halves, there should be theoretically complete

loss of sensibility on both sides of the body, whilst the motor power should remain intact; and, according to Brown-Séquard, this actually occurs, but there is some difference of opinion upon the point. The discrepancy may perhaps be due to the circumstance that a very small column of grey matter remaining uninjured on either side is sufficient to conduct sensory impressions. Yet it is remarkable that the grey matter is not itself sensitive to ordinary stimuli.

A vertical section made through the spinal cord for a short distance at the decussation of the pyramids, will cause loss of motion on both sides of the body, whilst the perception of sensations is comparatively little affected.

The **centres existing in the spinal cord.**—Certain acts require for their due performance the co-ordination of many muscles. If these do not contract in a regular and orderly manner, the act is imperfectly performed. The segment of the nervous system which governs and regulates the movements is termed a reflex centre. Proceeding from below upwards, the following centres have been demonstrated in the cord:

1. The ano-spinal centre, or centre controlling the act of defæcation.
2. The vesico-spinal centre, regulating micturition.
3. The erection centre, } or genito-spinal centre, in
4. The ejaculation centre } male.
5. The parturition centre, in the female.
6. The vaso-motor centre.
7. The vaso-dilator centre.
8. The sweat centre.
9. The cilio-spinal centre.

The first five centres are situated in the lumbar region; the sixth, seventh, and eighth extend through a large portion of the cord; and the last occupies the lower part of the cervical and upper part of the dorsal region.

The **functions of the medulla oblongata.**—The medulla oblongata may be regarded as a collection of reflex centres, traversed by fasciculi of white fibres in all directions. (*See* Klein's "Histology," p. 142.) It is inferior to the brain proper in possessing no power of initiating movement, apart from the cardiac and respiratory reflex movements, the mechanism of which is contained in this part of the nervous system. Even in the frog, if time be given for the prostration caused by the removal of the brain to pass away, no movements are observed, except as the result of the application of some external stimulus. The body assumes the position it takes up naturally when the animal is at rest, and if carefully protected from external stimuli, remains immovable; but if stimuli be applied, the reflex movements induced are extraordinarily complicated, and closely simulate those of the will. If laid upon its back it endeavours, though generally unsuccessfully, to turn on its belly. If placed in water, it swims, and comes to the surface to breathe. If the water be gradually warmed, it makes efforts to escape. In the higher animals, sections made through the pons, or junction of the pons with the medulla oblongata, are attended with so much prostration from pain and bleeding that the results are not very trustworthy; but movements of various kinds not involving change of place, and cries in response to strong stimulation of sensory nerves, have been observed. The animals are of course rendered blind, and deprived of the power of smell, but hearing is to some extent retained.

Centres in the medulla oblongata.—These are both numerous and important.

1. Centre for suction.	Sensory fibres.	Fifth and glosso-pharyngeal.
	Motor fibres.	Facial, hypoglossal, and motor fibres of third division of fifth.

2. Centre for mastication.	Sensory fibres.	Fifth and glosso-pharyngeal.
	Motor fibres.	Facial, hypoglossal, third division of fifth.
3. Centre for insalivation.	Sensory fibres.	Glosso-pharyngeal and fifth.
	Motor fibres.	Facial, sympathetic.
4. Centre for deglutition.	Sensory fibres.	Fifth, glosso-pharyngeal, and vagus.
	Motor fibres.	Spinal accessory, vagus, hypoglossal, and sympathetic.
5. Centre for vomiting.	Sensory fibres.	Fifth, glosso-pharyngeal, vagus, and afferent fibres from many organs; stomach, intestines, and kidney.
	Motor fibres.	Spinal accessory, vagus.
6. Centre for closure of eyelid.	Sensory fibres.	First division of fifth.
	Motor fibres.	Seventh or facial nerve.
7. Centre for dilatation of pupil, and for smooth muscle of orbit.	Sensory fibres.	Optic, fifth.
	Motor fibres.	From the spinal cord which first enter the sympathetic nerve.
8. Respiratory centre.	Sensory fibres.	Vagus, sympathetic.
	Motor fibres.	Phrenics, spinal nerves.

9. Centre for inhibition of cardiac movements. (This has already been considered, page 226.)
10. Centre for accelerating cardiac movements.
11. Vaso-motor centre.
12. Vaso-dilator centre.

The **functions of the basal ganglia.**—Several ganglionic masses are situated at the base of the brain, which, both in their mode of development and in their anatomical and physiological characters, may be regarded as a continuation of the spinal cord and medulla oblongata. These are the grey substance of the pons; the corpora quadrigemina; the grey substance of the cerebral peduncles; the optic thalami; and the corpora striata. The functions of these parts are very imperfectly known, for, lying deeply, great damage to other parts and prostration occurs in animals in which they are subjected to direct experiment, rendering the observations made upon them very untrustworthy; whilst as they occupy an intermediate position between the cerebral hemispheres and the

spinal cord, and many of the fibres connecting these parts pass through them, it is difficult to distinguish, in experiments, what effects are attributable to the injury inflicted on the special centre under examination, and what to the lesion of the connecting fibre. Some points may, however, be regarded as determined, partly from the results of experiments, partly from a consideration of their histological characters and anatomical connection, and partly on pathological grounds, that is, from observation of the symptoms of disease limited to these structures. Still more would probably be gained if we possessed accurate knowledge of their ontological development, and of their comparative anatomy.

Functions of the pons.—The structure of the pons shows that it is composed of masses of grey substance traversed both longitudinally and transversely by white fibres. The superficial portion is chiefly composed of transverse fibres acting as a commissure between the hemispheres of the cerebellum, whilst the deeper parts present longitudinal fibres that are partly continuous with the motor, partly with the sensory fibres of the spinal cord. Stimulation of the pons produces, therefore, pain and convulsions, whilst section occasions paralysis of sensory, motor, and vaso-motor nerves, as well as compulsory movements. Complete section, of course, abolishes all influence of the higher centres on the body. There is good reason, therefore, for believing that it is a centre for the co-ordination of movement.

Functions of the corpora quadrigemina.—The larger portion of the fibres of the optic tract penetrate the corpora quadrigemina of their own side; and experiment shows that if these bodies are destroyed on either side, blindness of the opposite eye results. If both are destroyed, the blindness is complete. The co-ordination of movements, which under

all ordinary conditions is so closely connected with visual sensations, is interfered with, and animals find a difficulty in preserving their balance. Electrical stimulation causes dilatation of the pupil, but the eye affected is not constant. Stimulation of the right anterior corpus quadrigemina causes both eyes to turn to the left, and *vice versa;* and if the stimulation be continued, the head also turns in the same direction. The reflex centre governing the contraction of the pupil when the eyes are exposed to light is situated in the corpora quadrigemina. The stimulus of light falling on the retina produces a wave of nerve force, which, travelling to the corpora quadrigemina on its own side through the optic nerve and tract is reflected by the third nerve to the lachrymal ganglion to which that nerve supplies the short root, and from which branches are given off to the sphincter pupillæ. Stimulation of the corpora quadrigemina causes contraction of the pupils, and fibres from both the optic nerve and the third nerve have been traced into these bodies. Other phenomena that have been observed are increase of blood pressure, retardation of the pulse, and deeper inspiration and expiration.

Functions of the cerebral peduncles.—The cerebral peduncles, like the pons, contain grey substance and longitudinally-arranged fibres, which are divisible into two groups, an anterior or inferior one, the *crusta;* and a superior one, the *tegmentum.** Little

* These two parts are separated from each other by a dark coloured mass of grey matter termed the *substantia nigra.* The crusta is chiefly composed of the pyramid fasciculi of the medulla oblongata, which have traversed the pons, and are passing onwards to the internal capsule of the cerebral hemisphere. The tegmentum is a continuation of the formatio reticularis, and consists of small longitudinal fasciculi of white fibres, crossed by transverse fibres. The longitudinal fibres ascend from the cord, and pass to the optic thalami, having previously received an accession of fibres from the ganglionic cells forming the red nucleus of

more can be said of the function of the cerebral peduncles with certainty than that they contain afferent and efferent nerve fibres, and that they are co-ordinating centres.

Functions of the corpora striata. — These bodies contain two masses of grey substance: one, the *nucleus caudatus*, intraventricular nucleus, or corpus striatum proper, is the larger; the other, or *lenticular nucleus*, is the smaller of the two. The functions, though certainly distinct, have not been differentiated. Electrical stimulation of the caudate nucleus produces, according to Ferrier, pleurosthotonos or lateral flexion of the body; whilst Nothnagel finds that destruction of the inner part near the ventricle, by means of a needle, or by the injection of a drop of chromic acid through a fine syringe on one side in rabbits, causes them, after a short interval, to execute violent running or leaping movements, or the "mouvements de manège," that is to say, "circus movements," the animal running round and round continuously in one direction, till it falls exhausted. He has hence termed it the "nodus cursorius." If the whole nucleus caudatus is destroyed, however, these effects are not observed. Similar experiments made upon the lenticular nucleus were always followed by motor paralysis.

Functions of the optic thalami. — These seem to be centres towards which many sensory fibres converge, for not only have they large connections with the optic tracts, but the greater part of the tegmentum of the cerebral peduncles, which appears to be in great measure a continuation of the sensory columns of the cord, enter them. Direct stimulation of them in animals by means of electricity has not been found to produce any movements.

the tegmentum. The cells forming the substantia nigra are deeply pigmented.

Lesion of them, which is not unfrequently observed in man as the result of hæmorrhage, produces anæsthesia, or loss of sensation, of the opposite side of the body; and if it be localised in the posterior third of the thalamus, visual disturbances have been, as might be expected, observed. It is particularly worthy of notice that various actions ordinarily regarded as voluntary may be performed by an animal from which the cerebral hemispheres have been removed. Thus, Longet found, that in a pigeon in which this operation had been performed the animal gave many indications of consciousness of light; for not only did the pupil contract, but the lids closed when a strong light was suddenly made to fall upon the eye, the animal having been previously kept in darkness; and when a lighted candle was made to move in a circle before it, the animal executed a corresponding movement with its head.

The general result of the observations made on the nuclei of the corpora striata and optic thalami is to favour the supposition that, like the anterior and posterior cornua of the grey substance of the spinal cord, they are respectively connected with the motor and sensory operations; and that whilst on the one hand they may act as independent centres of reflex action, and in this relation may be the centres for various automatic and instinctive movements which are commonly prompted and guided by sensations, they may also be subservient to the operation of the hemispheres, with the increase and development of which they, *pari passu*, augment.

Compulsory movements.—The two halves of the brain, basal ganglia and medulla oblongata, act together, under ordinary circumstances, in preserving a certain equipoise and harmony between the opposite sides of the body, which is rendered evident by the effects of lesions involving one half of these parts

Unilateral sections cause in many instances movements which are not under the control of the will of the animal, and seem to be the consequence of an irresistible impulse. In some cases the animal is compelled to run in a circle, in others to whirl round and round, in others to roll over and over. These movements sometimes take place towards, sometimes away from, the side on which the injury has been inflicted.

Functions of the cerebellum.—The size and complexity of the cerebellum increase with the number and variety of the movements that each animal is capable of executing, the organ attaining its maximum size in man, by whom the most complex actions are capable of being performed. If the cerebellum be cut away by successive slices, the animal soon becomes sullen and its movements irregular, and by the time the whole of the organ is removed, all power of springing, flying, walking, standing, or preserving the balance (that is, of performing any combined muscular movements which are not of a simply reflex character) is lost. On the other hand, neither the will nor the consciousness seems to be affected. Many pathological cases of cerebellar disease have been recorded in man, the distinguishing characters of which have been staggering gait, convulsions, and tendency to fall, or loss of balance. From these various circumstances the conclusion is drawn that the cerebellum is the *essential organ for the co-ordination of muscular movements.* Anatomical evidence is in favour of this view, for the cerebellum is directly connected with all the columns of the spinal cord, as well as with the basal ganglia and the hemispheres of the cerebrum. The cerebellum is insensitive to direct irritation. Some of the most remarkable examples of *compulsory movements* are observable on unilateral section of the cerebellar peduncles. In some cases the animal has been seen to roll over for many days

together at the rate of sixty times in a second. An obscure relation exists between the cerebellum and the sexual functions.

It is reasonable to suppose that in the performance of a particular action an impulse is propagated from a few, or even from one ganglion cell of the cortex of the cerebral hemispheres, which communicates directly with a centre composed of many cells capable of bringing into simultaneous action numerous muscles.

Functions of the cerebrum.—The hemispheres of the cerebrum are the seat of all psychical processes, that is to say, they contain the higher centres which minister to thought and volition. They are the centres of memory. In them are performed all operations of reason and judgment, and they initiate the voluntary impulses which consist in the intelligent adaptation of means to ends. Usually acting coincidentally, they are probably capable by practice of being brought into separate action. Their removal appears to plunge the animal into a deep sleep, from which no irritation ever seems able to rouse it into full activity, although it may give manifestations of consciousness. It is worthy of observation, however, that large portions of the brain may be destroyed by disease, or removed in consequence of accidents, without very material impairment of function, so that it is possible that a process of substitution may take place.

Two opinions are entertained in regard to the action of the brain. Both agree in considering that the brain is the instrument of all the higher intellectual or psychical functions. From the one point of view, however, it is maintained that the nerve cells are accumulated in certain regions to form centres, the definition of which is, indeed, obscured by the complexity of the communications intervening between themselves and between the centres situated on lower planes, as those of the basal cerebral ganglia and the

ganglia of the medulla oblongata and spinal cord, but which act like other centres in a reflex manner to stimuli that affect them from without or from within. From the other point of view it is considered that although the brain is physically a part of the nervous system, it is to be regarded as the organ through which the mind of man operates, as a whole, and as having altogether superior functions to any other part of the nervous system, directing, controlling, and otherwise influencing the lower centres. It is regarded as the organ of the will, which acts in a mode that is incomprehensible indeed, but which is evident enough, through the cerebral cells.

The difference of opinion in regard to the mode of action of the brain between physiologists is analogous to that which exists between materialists and spiritualists. To illustrate the views by an example. A man voluntarily thrusts forth his arm, or he determines to think of some object, as a horse; and says, See; I believe in the independence of the will. I choose to thrust forth my arm, and I do so; I choose to direct my thoughts to a horse, and I do so. The spiritualist contends that herein is the evidence of a something separate from the body, the mind, which has called into play the centres that are capable of exciting the contraction of the extensor muscles of the arm, or those which, when collectively excited, make up our idea of a horse. He maintains there need be no antecedent stimulus, but that the mind has originated within itself the necessary conditions for the acts in question.

The materialist, on the other hand, sees in such operations nothing more than reflex acts, though of a somewhat higher or complex nature than those ordinarily performed by the spinal cord or medulla oblongata. The man, he maintains, does not thrust forth his arm, or think of a given animal, until other groups of cells have been excited or aroused, either by

the mere stimulus of discussion or by the sequence of a train of ideas, each of which is immediately related to that which has preceded it. From this point of view there is no such thing as free will. The acts and thoughts of a man are the results partly of original and hereditary confirmation, partly of the direction of his own occupation and pursuits; and were it possible for us to know the whole antecedents of the individual, it would be possible to predict what his conduct would be in any given crisis. Instincts may be regarded as habits which have become hereditary and fixed by natural selection. The consideration of these questions is not, however, adapted for an elementary book, and must be looked for in larger treatises. It was long considered that it was impossible to excite the brain to the manifestation of its powers by direct stimulation of any kind. But the experiments of Hitzig and Ferrier have shown that this conclusion was the result of imperfect observation, and that the application of electric currents to different parts of the cerebral surface is followed by movements of very various kinds, and by evidences of sensation, whilst the destruction of these regions occasions loss of sensation in the one case, and loss of voluntary control over the muscles that respond to the stimulation in the other. In Ferrier's experiments the electric stimulus employed was that derived from a single Daniell's cell, which is strong enough to be just borne when applied to the tongue. The application of the electrodes produces very decided movements; and if they are shifted over a sulcus to a different convolution, a different set of muscles is immediately called into action. The following regions have been mapped out by Ferrier in the brain of a monkey: (Figs. 16 and 17) Stimulation of 1 produces movement of the hind limb as in walking; 2, complex movements of the hind leg, especially adduction of the foot to the middle line;

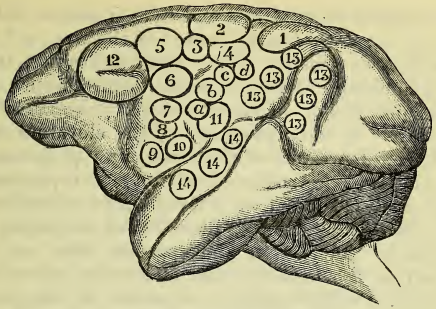


Fig. 16.—Side View of the Brain of a Monkey, showing Localised Areas.

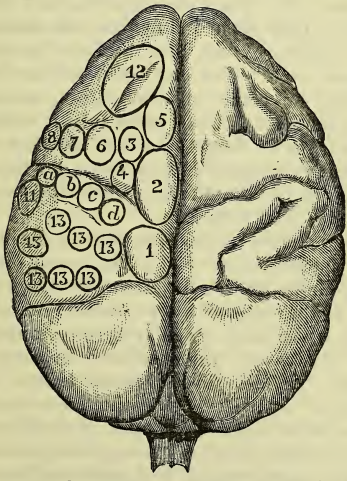


Fig. 17.—Diagram of the Brain of a Monkey, seen from above, with Localised and Numbered Areas. The stimulation of each of them is followed by the results stated in the text under the corresponding numbers.

3, movements of hind foot and tail; 4, action of latissimus dorsi; 5, extension forward of the arm; *a*, *b*, *c*, *d*, successive movements of the hand and wrist, terminating in closure of fist; 6, action of the biceps; supination and flexion of the fore-arm; 7, action of the zygomatici; 8, conjoint action of the elevators of the upper, and depressors of the lower, lip; 9, opening of the mouth and protrusion of the tongue; 10, retraction of tongue; 11, action of platysma; 12, elevation of the eyebrows and eyelids, dilatation of the pupils, and rotation of the head to the opposite side; 13, eyes directed to the opposite side, and either upwards or downwards, with, usually, contraction of the pupils; 14, retraction of the opposite ear, head turning to the opposite side, the eyes widely opened, and the pupils dilated; 15 (not given in figures, but corresponding to tip of uncinate gyrus), torsion of the lip and nostril of the same side. The antero-frontal and occipital regions give no result on stimulation, nor does the island of Reil react. Upon the whole, it would appear that the centres of motion for the anterior and posterior limbs are situated in the convolution immediately surrounding the frontal fissure, which runs transversely to the longitudinal fissure.

Ferrier believes he has been able to localise certain regions of special sense; viz., 1. The *psycho-optic centre. Blindness* results from destruction of the angular gyrus (Ferrier), or the occipital lobes (Munk); but this is only temporary if the other angular gyrus is uninjured; if both are destroyed, the blindness is complete and permanent. 2. The *psycho-acoustic centre. Deafness* results from destruction of the superior temporo-sphenoidal convolutions. 3. *Loss of tactile sensibility* results from destruction of the hippocampus major and hippocampal convolutions. 4. *Loss of smell* results from destruction of the subiculum cornu ammonis, or tip of the uncinate convolution. 5. *Loss of taste* results from

destruction of the lower part of the temporo-sphenoidal lobe.

The **speech centre.**—One of the best defined regions, and that one which has been longest known, is the region through which speech is effected. It is the third left frontal convolution, which is in part continuous with the island of Reil. In rare instances lesions have been observed in the right third frontal convolution, which have led to loss of speech. Most men, therefore, are left-brained speakers, just as most men are right-handed, which is also associated with special development of the left brain. In the cases where lesion of the right third frontal convolution has caused loss of speech the individuals have also been left-handed.

The **duration of psychical processes.** — It has been ascertained that a visual impression induced by a constant stimulus is not constant in intensity, but increases from zero till it reaches a maximum, and then gradually diminishes. The same holds in regard to the ears, except that it is not known whether after a certain time the sensation diminishes in intensity; and it is observed also in the perception of gustatory and olfactory sensations. In the latter cases the process is so slow that it becomes highly probable that it is to be referred to conditions of the terminal apparatus, rather than to peculiarities of the cerebral nervous organs. It is known that for a visual stimulus to give a continuous impression there must be more than twenty-four impulses in the second; yet if the optic nerve be directly stimulated by means of sixty shocks of electricity per second, the impression is by no means continuous, though the latter stimulus may be less intense than the first. Here, again, it may be deduced that the tardy course of visual sensations is due to the slow process of excitation of the retina, and not to slowness of perception on the part of the brain. It

is to the different rapidity with which the terminal organs respond to impressions, though partly also to the different speed of conduction in the nerves, that the difference in fixing the exact time of the occurrence of any phenomenon is due. That such difference exists has long been known to astronomers, by whom it is recognised, and allowed for under the name of *personal equation.* In astronomical observations it is of great importance to fix the precise moment when, for example, the transit of a star takes place across the hair line of a telescope, and this is done by comparing what is seen with what is heard, as the click of a clock; or by pressing the knob of an electric apparatus at the moment of observation of the transit; but if one observer fixes the moment of transit as occurring at a given moment, another observer may make it one half second or even a whole second later. In this case the time as given by the last observer must have a certain deduction made, when compared with the first, in order that correct results should be obtained.

Rapidity of perception. The smallest difference.—How quickly can two sensory impressions follow each other, and the succession in point of time be correctly stated? The answer to this question gives the smallest difference. In the case of the visual sense, where the same part of the retina is stimulated, this has been determined by rotating a disk with black and white sectors before the eye, and it has been found, that with ordinary daylight the retina must be stimulated about twenty-four times in the second, before it assumes a uniform grey aspect, that is, for the smallest difference to be surpassed. In this way a smallest difference of $\frac{1}{48}$th second is obtained. It is not necessary, however, that the white sectors should be of the same size as the black, in order that with twenty-four stimuli in the second a uniform grey should appear; which shows that it is the alternation

and not the duration of each impression which is of importance. When different parts of the retina are affected, as when a point is watched where two electric sparks can be made to appear quickly, one after the other, the images of which upon the retina are not separated by a greater interval than 0·011 mm., and which, therefore, both fall on the yellow spot, it can be determined which spark first appears, when the intervening period is not more than 0·044 sec. In the case of the ear, when the sound attended to is that caused by two electrical sparks quickly succeeding each other, it can be perceived that there are two, and that one is earlier than the other, when it precedes it by no more than 0·002 sec. It is remarkable that the minimum difference for one ear when both sounds affect it, is smaller than when one sound affects one ear, and the other the other ear; as is shown by the fact that a slight inequality of beat can be distinctly perceived when two watches are held before the same ear, which is imperceptible when one watch is held before one ear, and the other before the opposite one. In regard to tactile impressions, great differences appear to exist in regard to the shortness of the interval between a series of tactile impressions, in order that they should no longer be perceived to be discontinuous but fused into one. Preyer stands alone in stating, that from twenty-eight to thirty-eight beats per second give a continuous sensation. Valentin gives the limits as varying from 480 to 640, and V. Wittich places it at about 1000.

Recognition of simultaneous impressions on eye and ear.—If an electric spark be made to appear, and simultaneously a bell be struck, the coincidence of the two in point of time is not easily or certainly recognised; and if it is unknown whether they are precisely simultaneous or not, the subject of the experiment will often rightly state that they are

simultaneous, but often also that the sound precedes the spark; he will rarely state that the spark precedes the sound. In a large series of experiments, in which a judgment has to be formed between the precedence of a sight or sound, it has been found that the perception of sound is a trifle earlier than that of light. The ear is quicker than the eye.

Reaction time.—By this is meant the time between the application of a stimulus to some sensory nerve, and the time when a signal is made to indicate that it has been perceived. This experiment may be conducted in a variety of ways. By Helmholtz and others it has been done by applying a stimulus to one hand, and signalling with the other; and the results of observations made by different experimenters have given very different results. One observer, for example, found it to be 0·1087 sec., and another 0·1911, or nearly twice as long. But the experiment may also be conducted by stimulating other sensory nerves, as the eye and ear, whilst still making the hand signal. The sudden appearance of a light required a period of 0·1139 sec. to be signalled, and the occurrence of a sudden sound 0·1360 sec., by the same observer.

Instead of the hand, the lower jaw and foot have been made to signal. The reaction time from the eye stimulated by an electric spark to the lower jaw is 0·1377 sec., and from eye to foot, 0·1840 sec.

Personality has much to do with the rapidity of propagation of nervous impulses. Thus, an intelligent young man, much interested in this question, was compared with an old man of seventy-seven from the Union, and it was found that, whilst the reaction time from hand to hand for the youth was 0·3311 sec., for the old man it was 0·9952 sec. But practice can be shown to be of importance, for experiments continued for more than half a year

with the same old man showed extraordinary improvement, since in June his reaction-time was as above, but with ten days' practice it had fallen to 0·3576 sec., and in January of the following year it was only 0·1866 sec. Exhaustion of the attention prolongs the reaction time. Intensity of stimulus abbreviates it. The processes that are included in the reaction time are numerous. They are: 1. The conduction of the stimulus or sensory impulse through the nerve and the spinal cord to the central organ; 2. Conversion of the sensory impression into a motor impulse; 3. Centrifugal conduction of the motor impulse through the spinal cord and motor nerve; 4. Liberation of the muscular movement. If, in addition to the mere reaction-time, a judgment has to be formed (that is to say, that one of two colours is presented to the eye, or two sounds to the ear, and a signal corresponding to each has to be touched), it is found that a period of 0·036 sec. has to be added to the reaction period.

Sleep.—Sleep consists in the more or less complete suspension of the psychical operations, whilst the purely vegetative processes are continued, though usually with diminished energy. The heart, for example, beats less frequently, the respirations are slower, and the digestive operations are less active. The cause of sleep is unknown. It is probably primarily associated with the great cosmical alternation of day and night, and with the diminished molecular activity that takes place in the cerebral cells during the hours of darkness. It may also, as Dr. Capper believes, be in part attributable to altered conditions of the cerebral circulation, and perhaps also to diurnal variations in the amount of oxygen absorbed. Its duration varies greatly with age. The infant and old person sleep half their time away, whilst in mid age, especially when mental strain is experienced and

work has to be done, five or six hours are all that is needed. The conditions most favourable for sleep are moderate fatigue both of mind and body, recent but moderate supply of food, quietude or monotonous sound, absence of anxiety, and habit. It has been observed in some pathological cases in which several of the senses have been abolished (as those of touch, sight, smell, and taste, whilst hearing has been retained) that the suppression of this remaining sense rapidly induces sleep. In many persons sleep is very profound, and some time elapses on being awakened before they can gather their senses together; whilst others sleep with their faculties about them, or at least within ready call, so that the slightest noise or touch awakes them. Such persons are often capable of fixing very accurately the time when they shall awake.

Guiding sensations.—In order that the will should call a definite group of muscles into play, it must be cognisant of the position of the parts about to be moved, and of the state of the muscles it is about to cause to contract. This knowledge is afforded by guiding sensations, the existence of which in health has been deduced rather from the observation of the phenomena of disease than by direct evidence under normal conditions, for it is found that if the sensibility of any part be lost, or if the guiding sensations derived from the visual and aural senses be suddenly removed, great difficulty is experienced in the performance of movements that seem, under ordinary conditions, to be executed quite unconsciously. Many examples of this might be cited, but amongst others may be mentioned that in certain conditions of ataxia, though there may be no loss of power in the muscles of the limb, the patient walks with difficulty, unsteadily, and with tottering gait, because, in consequence of the loss of tactile sensibility in the feet, he does not exactly recognise their

position, and is therefore unable to plant them properly. In like manner, a woman is unable for any length of time to hold her child in her arms, but the sense of position of the brachial muscles being lost, they unconsciously yield to gravity, and the arm falls. The guiding sensations derived from the eye are those upon which we chiefly depend in our ordinary life; and every one must have experienced the sense of insecurity, and the difficulty of pursuing a straight course, when the eyes are blindfolded. It is interesting to observe, moreover, that guiding sensations derived from one sense may supply the loss of those from another, for in such cases of ataxia as those above mentioned, the deficiency of the muscular sense may be made good by the visual, standing and walking, or the preservation of the child, being accomplished, provided the patient looks at the limbs. A sense of vertigo or insecurity may, in a similar manner, be produced by the supervention of sudden deafness. The precise adjustment of the muscles of the larynx which is required for the emission of vocal sounds is effected through the auditory sense, for when this is absent, vocal intonation is learned with difficulty through the eye, and the voice is never pleasing. It would be impossible for a person born deaf to become a brilliant or even moderately good singer. Many habitual actions are, when once commenced by the will, maintained by the existence of guiding sensations. Thus, in mastication the act may be continued, whilst the mind is wholly absorbed in a train of thought, and directs no attention to the process, though there is a disposition in such cases to continue to turn the same morsel over and over in the mouth rather than to proceed to the next act, of deglutition. Guiding sensations may occasionally be antagonistic, and the movements may then become uncertain. In walking across a plank at a great height, although the

feet are in contact with solid material, yet the sense of insecurity occasioned by the unusual condition of not being able to see or fix any object with the eye between the near plank and the remote ground, renders the movements of the limbs and the maintenance of the equilibrium exceedingly difficult, especially if there be any swaying of the plank itself; yet no difficulty is experienced in walking along a narrow plank in the flooring of a room, when all accessory guiding sensations are brought into action.

Ideas.—Ideas are to be regarded as a mental state or representation, which assumes the character of an independent intellectual reality (Carpenter). In forming them, the mind is determined by the nature and intensity of the various affections of its consciousness which have been excited by the object; and as these depend in part upon the original constitution of the cerebrum, and in part upon the mode in which its activity has been habitually exercised, it follows that the ideas of the same object or occurrence which are formed by different individuals may be widely discrepant. There are some ideas which are so constantly present in every soundly constituted mind that they have been named primary beliefs, or fundamental axioms. The chief of these are: Belief in our present and in our past existence; belief in the external and independent existence of the causes of our feelings, leading us to distinguish the *ego* from the *non ego;* the belief in the existence of an efficient cause for the changes we witness around us; the belief in the uniformity of the order of nature; and the belief in our own free will.

Emotions.—These may be regarded as being constituted by certain classes of ideas to which feelings of pleasure or of pain are attached. They include the mental states of joy, hope, surprise, fear, and the like. They are apt to lead to the liberation of movements

which are peculiarly characteristic of the emotion experienced.

Laws of mental association of ideas.—The most important of the laws which have been laid down by psychologists in regard to the succession of our mental states, are those which relate to the association of ideas. The first of these is the *law of contiguity*, which is to the effect that two or more states of consciousness habitually existing together or in immediate succession, tend to cohere, so that the future occurrence of any one of them restores or revives the other. Good examples of this may be drawn from the memory of any common object, such as an orange, the idea called up by the sound of the word blending together many attributes of the fruit, as colour, surface, form, consistence, and even internal structure, which, by having been frequently presented coincidentally to our senses, have grown together in the mind, and recur together when one or other of them is thought of. Of this law of contiguity, we have, Dr. Carpenter remarks, a most important example in the association which the mind early learns to form between successive *events*, so that when the first has been followed by the second a sufficient number of times to form the association, the occurrence of the first suggests the *idea* of the second; if that idea be verified by its occurrence, a definite *expectation* is formed; and if that expectation be unfailingly realised, the idea acquires the strength of a *belief*. And thus it is that we come to acquire that part of the notion of "cause and effect," which rests upon the "invariability of sequence," and to form our fundamental conception of the uniformity of nature.

Law of similarity.—This law is to the effect that present sensations and thoughts have a tendency to revive preceding states of consciousness which resemble them. Having once seen and eaten a bunch

of grapes, we recognise a second bunch, though it may be much larger or smaller, and even though the colour may be different, the form of the individual berries, as well as their arrangement, predominating over the colour, and rendering us certain, when the colour might engender a doubt. Some minds, however, take note of differences with greater quickness than of similarity. Minds that are capable of perceiving minute points of resemblance or of difference, like that of Linnæus, are well adapted to classify and arrange natural objects; and the recognition of similarity and dissimilarity between mental images and ideas is a characteristic of the highest order of minds, such as those of Shakespeare and Bacon.

There is yet another law, termed the **law of constructive association,** which is the foundation of the imagination, and examples of which are found in those cases in which, from an outline or a sketch, we build up a complete form, or in which we combine two or more dissimilar ideas into a concordant whole.

CHAPTER XV.

THE SENSES.

Psycho-physical law.—Our sensations, as Helmholtz has pointed out, are only the signs of external objects from which they are totally different, but which our judgment has learned to interpret always in the same sense. Sensations differ in kind and in intensity. Those of hearing, sight, and of the other special senses as they are termed, differ in kind, or are specifically distinct from each other, and no comparisons, except of a very recondite nature, can be instituted between them. The variations in the intensity

of each kind of sensation are, on the contrary, constantly being brought under our consideration, and our judgment is being constantly exercised in determining their amount or degree. It has been found by experiment that for a difference to be recognised by the mind in the intensity of any sensation, the increase or the diminution, as the case may be, must bear a certain proportion to the total intensity of the sensation. This is the psycho-physical law.

Thus, in the case of the sense of pressure, estimated by placing weights on the well-supported hand, or in the case of weights balanced in the free hand, where the sense of pressure is combined with that of muscular effort, it is found that, in order that a difference should be perceived, the same fraction of the total weight must be added or taken away whether this be grains or pounds. In each case the proportion must be at least as 29 : 30 before a difference can be perceived. The psycho-physical law, in fact, enunciates the relations which exist between the intensity of physical agents and their psychical result, sensation (Nuel). The proportion is not, however, the same in other senses; thus, in the case of light it is as 100 : 101; for if we suppose a screen of a uniform white divided into two halves, each lighted by one candle, and if now one of the candles be approximated to the screen, the intensity of the light will be increased in that half, and if the distance of the candle from the screen be noted at the moment when we perceive a sensible augmentation in the light of that half on which it falls, we shall find that the distance of one candle is just $\frac{1}{100}$th more than that of the other candle. But it matters not whether the number of candles by which each half is illuminated be two, or ten, or one hundred, for it will be found that a difference is always perceived when the brightness of one half of the screen is one-hundredth more

than that of the other. This law is, of course, true only within certain limits; with very heavy or extremely light weights, or with such extremely vivid lights as that of the sun or the carbon points of a powerful electric battery, no difference would be perceived. Even with the various sensations of the same sense, some difference in the proportion occurs. Thus, in the case of luminous sensations, in order that a difference of intensity in red should be perceived, the difference in intensity must be as much as 70 : 71; in orange as 78 : 79; in yellow and green as 286 : 287; in blue as 212 : 213; and in violet as 109 : 110. We perceive slight variations in intensity in yellow and green far more readily than in red.

The **Eye.**—The eye is a camera obscura, and the images of external objects are depicted on the retina, which is a concave screen lining its posterior surface. The images here formed are inverted, and greatly reduced in size. The similarity of the eye to a photographic apparatus is rendered very striking by the circumstance that the rhodopsin, visual purple, or colouring matter of the rods and cones, is bleached by exposure to light, so that, by the application of appropriate chemical agents, the image of a brightly illuminated object can be fixed, and rendered apparent for some time.

The **optic axis.**—This is a line which passes through the nodal point and the centre of the cornea; if prolonged backwards, it falls upon the retina on the inner side of the yellow spot.

The **visual line.**—The visual line joins the macula lutea with the point on which the eye is fixed. It passes through the cornea a little to the inner side of its centre, and therefore forms an angle with the optic axis, which is termed the angle α. This angle does not exceed in the normal eye 4° or 5°. In looking at a distant object, as a star, the visual lines are

parallel, and the optic axes are directed outward; but since we judge of the position of the eyes of another person by the position of the centres of the cornea, the eyes appear to diverge slightly, or in other words it may be said that there is slight apparent strabismus. That there is no real squint is shown by covering, when a distant object is regarded, first one eye and then the other, with the hand, when it will be found that neither eye alters its position.

Field of vision.—This is the area which can be seen by each eye, when the head and body, being maintained in a fixed position, the eye is rotated to the utmost in the different meridians. The field of vision is most extensive below and on the outer side, being limited above by the brow, below by the cheek, and to the inner side by the nose. The limits are, for each eye: Outwards, 45°; downwards and outwards, 47° to 50°; inwards, 45°; upwards and inwards, 45°; downwards, 50° to 55°; upwards and inwards, 38° to 40°; upwards, 43°; upwards and outwards, 47° to 50°.

Visual angle.—This is the angle included between straight lines drawn from the extremities of the object to the nodal point (*o*, Fig. 18) of the rays refracted by the media of the eye, which is situated a little behind the centre of the lens. Our estimate of the size of any object is mainly dependent upon the visual angle under which it is seen. The size of the visual angle depends, first, on the size of the object, and, secondly, on its distance from the eye. The distance remaining unaltered, the size of the visual angle varies with the size of the object; and on the other hand, the size of the object remaining the same, the size of the visual angle diminishes with the distance of the object.

In Fig. 18, A *o* B or the angle *o* is the visual angle of the line A B. The retinal angle *b o a* is equal to the visual angle, and is formed by the same

lines continued beyond the nodal point *o*, and it is limited by the extremities of the image formed on the retina. It is seen from the figure that objects of different magnitude, *e*, *d*, *c*, placed at different distances, may be seen under the same angle, and in the absence of other means of correcting the impression,

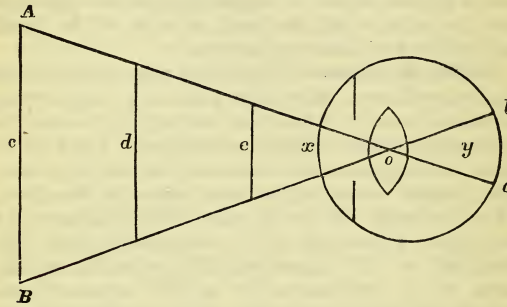


Fig. 18.—The line A B has a visual angle *x*, and a retinal angle *y*, both of which are identical with the visual angles of any lines drawn parallel to A B between the lines A *o*, B *o*.

may be all considered to be of the same size. It also shows why the image is reversed.

Sharpness of vision.—This corresponds with the defining power of the eye, the power which the eye possesses of distinguishing two points as separate. It is measured by the smallest angle under which two objects of definite and constant size can be distinguished from each other when separated by an interval of corresponding size to the diameter of one of the objects, or by the determination of the smallest retinal image, the form of which can be perceived by the eye, providing it is not a line. The smallest object that can be seen at the distance of a foot is $\frac{1}{250}$th of an inch, which subtends an angle of about

1 minute, certainly not less than half-a-miuute. The retinal image corresponding to a visual angle of one minute has been calculated to be about 0·004 mm., or $\frac{1}{6000}$th of an inch, which is the diameter of a cone, but brilliantly illuminated objects of much smaller size may be seen. It follows, then, that the smallest object that can be seen at two feet is $\frac{2}{250}$ths of an inch; at five feet, $\frac{5}{250}$ths of an inch, and so on. In ophthalmic practice, the meter is taken as unity of distance, instead of the foot, and letters have been selected of a certain size, usually subtending 5′, and the patient's sharpness of vision is tested by determining at what distance he can name the letters correctly. Donder's formula, $V = \frac{d}{n}$, enables the sharpness of vision to be immediately estimated, for V, which stands for sharpness of vision, is measured by a fraction of which the *numerator d* is the distance in meters at which a given letter can be read, whilst the *denominator n* is the number of meters at which it ought to be read by any one possessing average or normal acuity of vision. Thus, a letter which by experiment it has been ascertained ought to be read by a normal eye at 12 meters from the subject, is placed before the person to be tested. If he reads it at 12 meters, his vision is perfect, $V = \frac{12}{12} = 1$; but if he can only read it at 6 meters, then his vision is expressed by $V = \frac{6}{12} = \frac{1}{2}$; if only at 4 meters, $V = \frac{4}{12} = \frac{1}{3}$, and so on.

The greater sensibility of the macula lutea is possibly due to the anatomical arrangements and connections of the parts. Sulzer estimates the number of nerve fibres in the optic nerve at about half a million, whilst the number of rods and cones is about three and a half millions. It has been suggested as not improbable that at and near the macula each cone is in direct connection with the brain by a single nerve

fibre, whilst near the equator of the eye two or more cones and rods are supplied by a single fibre, and near the ora serrata one fibre is distributed to many of these elements.

The sharpness of vision is modified by various circumstances. It is greater in youth, and becomes gradually less as age advances. It is greater when the object is well illuminated (provided the illumination is not excessive) than when indifferently lighted. The size of the pupil influences the sharpness of vision; for a large pupil, by flooding the retina with light and increasing the circles of dispersion, impairs vision. Wild races have usually very sharp vision.

Direct and indirect vision.—Vision is said to be direct when the image of the object falls on the macula lutea; it is indirect when it falls on any other part of the retina. It is found by experiment that the sharpness of indirect vision rapidly diminishes with the distance from the macula at which the image of the object is formed. Thus, if the sharpness of vision at the macula be taken at 1, at 5° from the macula, it is reduced to $\frac{1}{4}$; at 10°, to $\frac{1}{15}$; at 20°, to $\frac{1}{40}$; at 25°, to $\frac{1}{50}$; at 30°, to $\frac{1}{70}$; and at 40°, to $\frac{1}{200}$; and beyond this distance, though a moving object can be readily discerned, its form cannot be recognised with accuracy.

Marriotte's blind spot.—Though not ordinarily recognised, there is a spot in the field of vision which is incapable of perceiving light. This corresponds to the entrance of the optic nerve or optic papilla. It is situated 15° to the outer side of the point of fixation, and about 3° below the horizontal meridian.

Spherical aberration.—If a pencil of diverging rays of light fall on a lens made of homogeneous material, those that fall near the periphery of the lens are brought to a focus sooner than those that fall upon it near its centre. Hence the definition is imperfect. In optical instruments this defect has to be remedied;

and there are two modes in which it can be accomplished. In one, the curvature of the periphery of the lens is diminished as compared with the central part; and in the other, the density, and consequently the refractive power, of the periphery is diminished. The former is the most practicable method in art; and calculation has shown what is the precise curvature of the surface which enables a lens to give a perfectly defined image, and that it must not be the segment of a sphere, but of the end of an ellipsoid of revolution about its major axis. In the lens of the eye both of the above means of correction are employed; for in the first place, the outermost layers of the lens have less refractive power than the central and denser portions; and secondly, the curvature of the peripheral parts of the lens is less than the central part; in addition, the iris cuts off the most external rays, whilst the cornea contributes something to the effect, since its surface is really that of an ellipsoid of revolution around its major axis.

Chromatic aberration.—The different coloured rays of light possess different degrees of refrangibility. Red rays are least refrangible; violet rays are most refrangible. As white light is made up of rays of all degrees of refrangibility, it is clear that each colour will have its own focus; the violet rays will be brought to a focus first; the red, latest. Helmholtz has calculated, that for a reduced eye, *i.e.*, an eye reduced to its simplest condition for purposes of calculation, the focal distance of the red rays would be 20·524mm., whilst for violet rays it would only be 20·140mm., so that there is a difference amounting to about half a millimeter, or about one-fiftieth of an inch, and on a line of this length all the rays would be successively focussed. The result of this is that white objects situated at or beyond the far point have an edging or border of red, because the red rays have

not as yet met on the retina; whilst if they are nearer than the near point they have a violet edging, the violet rays having met and crossed. This defect in the structure of the eye is, however, so slight that it scarcely attracts notice. In optical instruments it is corrected by combining lenses of different dispersive power; as, for example, those of crown and flint glass. The bi-convex lens of a telescope made of crown glass possesses both great refractive and great dispersive power; but if combined with a concave lens of flint glass, the curvature of which is much less, its dispersive power may be neutralised without greatly diminishing its refractive power.

Use of the iris.—The iris is a thin highly vascular membrane, pierced by a hole in the centre, and continuous with the choroid at its periphery. The hole is the pupil, which is capable of undergoing great variations of size. It is surrounded by circular unstriated muscular tissue, by which it can be contracted to the size of a pin's head; and by radiating smooth muscular fibres, by which it can be expanded till it almost disappears behind the sclero-corneal junction. The sphincter pupillæ is under the influence of the third cerebral nerve; the dilatator pupillæ is under the influence of the sympathetic. The iris, in addition to these nerves, receives branches of the first division of the fifth nerve, which confers upon it acute sensibility. Light enters the eye through the pupil, and the first purpose fulfilled by the iris is to regulate the amount of light admitted into the interior of the eye. When exposed to bright light the pupil contracts by reflex action; the nervous circle being the retina and optic nerve, which is the *sensory* apparatus; a *centre* situated in the medulla oblongata; and the third nerve, which is the *motor* nerve. The brighter the light and the more sensitive the retina, the greater is the contraction of the pupil. Hence, in coming from a dark room into

bright sunlight the pupil contracts to the utmost, and pain may result from excessive stimulation of the fibres of the fifth nerve; and the stimulus radiating in various directions causes contraction of the orbicularis, and flow of tears. Light falling on one eye causes the opposite pupil to contract consentaneously. The stimulus for the dilatation of the pupil is the absence of light; and the nervous circle is the retina and optic nerve for the *sensory* apparatus, the cilio-spinal *centre;* and the sympathetic for the *motor* nerve. This centre can be excited by stimulation of other sensory nerves, acute pain causing dilatation of the pupil. It is stimulated also by imperfectly aerated blood, as is seen in conditions of dyspnœa.

A second purpose fulfilled by the iris is to aid in correcting the spherical aberration of the lens. The pupil contracts when the eyes are rolled inwards, or converged to see a near object. The effect of this is to cut off the outer rays of the divergent pencil, which, falling on the periphery of the lens, would be brought to a focus sooner than those passing through that body nearer its centre. The contraction of the pupil thus aids in making the images of near objects on the retina more clear and defined. The pupil contracts as an associated movement whenever the eye is rolled inwards; and as it turns inwards and upwards in sleep, the pupil is then also contracted.

The large supply of blood-vessels in the iris renders it almost an erectile organ. Hence, any circumstances causing congestion of the head, or repletion of the vessels of the eye, tend to produce contraction of the pupil. The escape of the aqueous humour on paracentesis of the cornea, by reducing the pressure under which the blood is moving in the vessels of the iris, leads to a rush of blood into them, and contraction of the pupil occurs.

Certain drugs possess remarkable powers of dilating,

and others of contracting, the pupil. The alkaloids of the Solanaceæ, atropin, hyoscyamin, daturin, as well as duboisin, cause, by paralysing the third nerve, wide dilatation of the pupil. Nicotin, pilocarpin, and especially eserine, on the other hand, cause, by paralysing the sympathetic nerve, great contraction of the pupil. It is probable that in addition to paralysing one set of nerve fibres, these agents stimulate their antagonists.

Near point and far point.—The points at which an object can be distinctly seen, when the accommodation is exerted to the utmost, is termed the near point, or *punctum proximum*, of the eye. It varies with the form of the eye, the strength of the ciliary muscle, and the elasticity of the lens. A child can bring an object within three inches of the eye, and still see it distinctly. Its power of accommodation is great, the ciliary muscle acts vigorously, and the lens is highly elastic, therefore it can bring strongly diverging rays to a focus on the retina. At fifty years of age an object cannot, as a rule, be distinctly focussed when it has been brought within twenty inches of the eye, for at that age the lens is of firm consistence, and its elasticity is reduced, whilst the ciliary muscle acts less energetically. As age advances, a book is held at a continually increasing distance from the eye, until at length the distance is so great that, although the letters are accurately focussed on the retina, the size of the image is so small that it can no longer be recognised. The loss of power in the ciliary muscle, and the diminishing elasticity of the lens, require to be supplemented by a convex glass, which renders the rays of light convergent.

The far point, or *punctum remotum*, for a normal eye is infinite distance, for the normal eye at rest is adapted to focus parallel rays on the retina, and it is only bodies that are at an infinite distance that emit parallel rays (Fig. 19).

How an image is formed on the retina.—Every convex lens presents a point, situated upon its axis, through which the axial ray of all incident pencils of light passes without deviation. This point is named the optical centre, and if the axial ray of each pencil be continued beyond the lens, it will pass through the corresponding image formed by the lens. Let AB

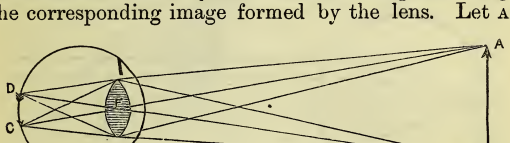


Fig. 18A.—Formation of Image on the Retina.

(Fig. 18A) be an arrow; it is seen that from each of the points A and B a pencil of rays proceeds towards the eye E. The axial ray of each pencil crosses the other at F, which is the optical centre, and being prolonged, meets the refracted rays of the same pencil at the focus C or D on the retina, thus forming an inverted image.

Accommodation of the eye.—In looking at two objects, one of which is nearer than the other, with a telescope, the position of the glasses has to be altered to see the nearer object, by drawing out the tube of the telescope. The same result can be obtained by thickening the glasses and rendering them stronger lenses. In the eye the latter plan is adopted. The muscle employed for this purpose is the *ciliary muscle*, or *tensor choroideæ* (10, 11, 12, Fig. 21). When the attention is fixed on a distant object the muscle is relaxed; the suspensory ligament of the lens is in action, and by its compression the lens is kept in a flattened state; the degree of flattening being just such as will allow parallel rays to be brought to a focus upon the retina. Thus we may consider the object to consist of several parts, as the barb, feathers, and

stem of an arrow. It is obvious from Fig. 19, that when the rays proceeding from each part are parallel, they will be exactly focussed on the retina, and that the image will necessarily be inverted. If, however, the object be situated near to the eye, as in Fig. 18A and Fig. 20, the rays proceeding from it will not be parallel, but

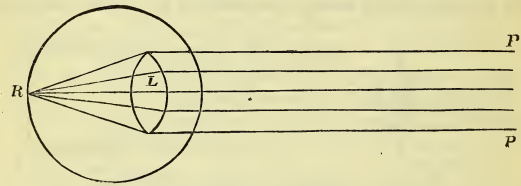


Fig. 19.—Accommodation of the Eye for Distance, Parallel Rays being brought to a Focus on the Retina. The eye is at rest, and no muscular effort is made.

L, Lens; P, parallel rays; R, retina.

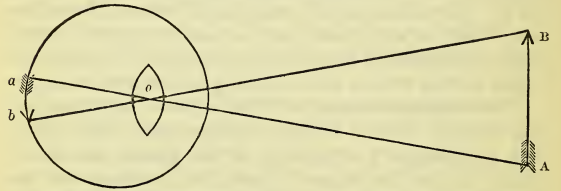
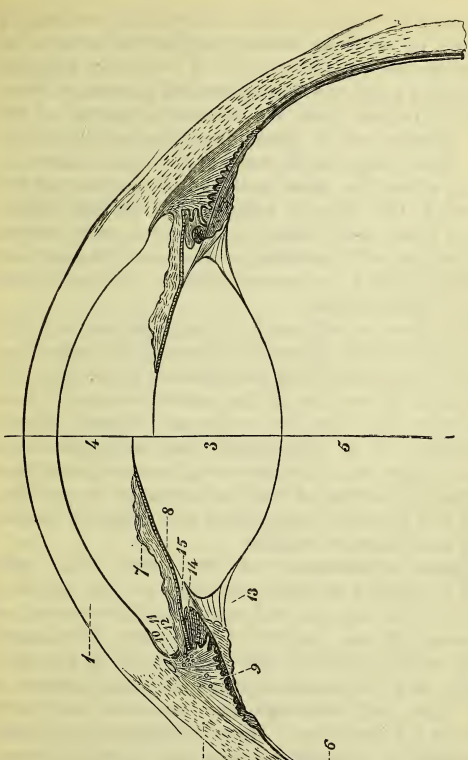


Fig. 20.—Accommodation of the Eye for Distance, Depiction of an Object on the Retina.

A B, Object; *a b*, retinal image; *o*, optical centre.

divergent, and divergent rays would not be brought to a focus so soon as parallel rays; in fact, would only be brought to a focus behind the retina, and not upon it. Either, therefore, the distance between the lens and the retina must be increased, or some change in the refractive power of the lens must be made; the latter plan is adopted, and it is accomplished by the action of the ciliary muscle. When this muscle contracts, the choroid membrane is drawn



1, Cornea; 2, sclerotic; 3, lens; 4, aqueous humour; 5, vitreous; 6, black choroid lying on the sclerotic, and covered by the retina; 7, iris; 8, black layer of pigment behind the iris, named the uvea; 9, ciliary muscle, meridional fibres; 10, origin of ciliary muscle; 11, 12, Circular fibres of ciliary muscle seen in section; 13, suspensory ligament of the lens; 14, tip of ciliary process; 15, posterior chamber of the eye.

Fig. 21.—Diagram of the Front Half of the Eye, to show the means by which Accommodation is effected.

forwards. The effect of this is to relax the suspensory ligament of the lens, which permits the lens to become more convex, the increase of convexity affecting the anterior part, and the degree of convexity being dependent in part upon the contractile power of the ciliary muscle, and in part upon the elasticity of the lens. This change in the form of the lens is shown in Fig. 21, where the upper half shows the state of the lens when the eye is adapted for distant vision; and the lower half when it is rendered more convex by the action of the ciliary muscle, and is therefore adapted, adjusted, or accommodated for the distant vision of near objects.

That there is really such a change in the convexity of the lens may be shown by observing the reflections from the cornea and from the surfaces of the lens, of a candle held to one side of the person observed, whilst he adjusts his eyes for near and distant objects alternately. It is then found that, while the erect corneal image remains stationary, the erect image from the anterior surface of the lens changes its position, whilst the inverted image from the posterior surface of the lens becomes smaller.

Optic constants of the eye.—The optic centre is situated in close proximity to the posterior surface of the lens, about 5 mm. behind the summit of the cornea, 15 mm. in front of the retina. The length of the antero-posterior axis of the eye is therefore 20 mm., and the posterior principal focal distance is at 15 mm., and the refractive power of the whole system is 6·5 dioptrics. These constants are of great importance in determining the size of a retinal image, for if we ask what is the size of the retinal image of AB (Fig. 20), supposing it to be 6 m. high, and situated at a distance of 10 m., the reply is that the two triangles AOB and *aob* give the proportion $\frac{x}{0{\cdot}15} = \frac{6}{10}$, x therefore = 0·09 m., which is the size of the retinal

image, or rather the size of the cord subtending the retinal image.

Scheiner's experiment.—This experiment demonstrates the necessity for accommodation, in order that single images should be formed on the retina. It consists in making two minute holes in a card (*see* Fig. 22) with a needle, the distance between which is less than the breadth of the pupil. If a single pin be stuck into a board and fixed (that is to say, looked at intently) through the card, a single image only is seen, because all the rays proceeding from it, though entering by two separate holes, are focussed on the retina; but if two pins, P and R, are now stuck into the board, one behind the other, and looked at through the holes, it will be found that when the proximal pin, or the one nearest to the eye, is fixed, the other, or remote one, is double, and *vice versa*. The reason of this is, that if the remote pin be fixed, and its image be formed distinctly on the retina, the more divergent rays proceeding from the nearer pin are not brought to a focus soon enough, but are focussed behind the retina; and as it is looked at through two holes, the image is double. On the other hand, if

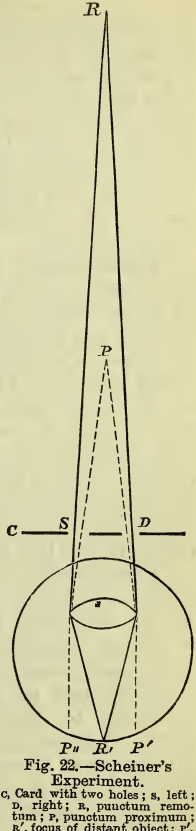


Fig. 22.—Scheiner's Experiment.

C, Card with two holes; S, left; D, right; R, punctum remotum; P, punctum proximum; R', focus of distant object; P', course of rays through dextral aperture from near point; P'', course of rays from near point through sinistral aperture.

the nearer pin be fixed, the lens is rendered a stronger one, and the rays coming from the more distant object are brought to a focus in the vitreous, or in front of the retina, and therefore cross. If the nearer pin is fixed, and the right hole is covered, the left-hand image of the double image of the more remote pin vanishes, because the rays have crossed in the vitreous. If the more distant pin is fixed, and the right-hand hole is covered, the right-hand image of the two images of the near pin vanishes, because the rays have not yet come to a focus.

Emmetropic eye. Normal or healthy eye.—The healthy eye is so constructed that parallel rays, or those coming from infinitely distant objects, are brought to a focus upon the retina when the eye is at rest and no exertion of the ciliary muscle is made. When near objects are looked at, the diverging rays which proceed from them are brought to a focus by the exercise of the muscle of accommodation. The most distant object which can be seen distinctly is an infinitely distant one, or one so distant that the rays are approximatively parallel. The nearest object that can be seen distinctly depends on the strength of the ciliary muscle and the elasticity of the lens.

Presbyopia.—The vision of old age. This is really only failure of the power of accommodation. In age, supposing the eye to have been originally of normal formation, distant objects are seen as well as in youth, except in so far as the eye, in common with the rest of the nervous system, reacts less vigorously to impressions, and is less sensitive to them. The presbyope sees near objects with difficulty. The images of these are confused and blurred, because he cannot exert his power of accommodation sufficiently to cause a distinct image to be formed on the retina; and this defect may be attributed in part to loss of power of the ciliary muscle, which is unable to draw the

choroid forwards, and therefore to relax the suspensory ligament, but partly also to defective elasticity of the lens, which, when the suspensory ligament is relaxed, does not become thicker, as occurs with the eye of a young person. The image of any luminous object situated within twenty or thirty inches of the eye (that is, within such distance that the rays proceeding from it are divergent) falls behind the retina, and no exertion that he can make enables him to obtain a picture of it on the retina. He requires convex glasses to enable him to see near objects distinctly; that is to say, the refractive conditions of his eye require that the entering rays should be rendered parallel before he can obtain a well-defined image. If in old age distant objects are not seen distinctly without a convex glass, the subject must have been hypermetropic.

Myopia.—Short-sightedness. In myopia the far point is at a measurable distance. The globe of the eye is elongated. Parallel rays are brought to a focus in front of the retina. Distant objects, therefore, are not clearly seen. On the contrary, rays more or less strongly diverging can be recognised distinctly. Hence, objects are brought into close proximity to the eye. Hence, also, concave glasses, which render parallel rays diverging, assist the vision of myopes; but in correcting the defect in practice the weakest power should be used compatible with clear vision.

It is often thought that myopic eyes improve with age, and those who are short-sighted congratulate themselves that they will see better as they grow older; but here also the same changes occur as in presbyopia. It is really a failure in the power of adjustment that gives a semblance of truth to the statement. The myopic person, as he advances in years, becomes unable to accommodate his vision for what was in youth his near point. He can only see objects distinctly when they are placed at his far

point. Hence he holds objects at a greater distance than formerly, and he appears to have improved to that extent; but it is only at the expense of his near vision. For objects beyond his far point, he must still wear, as he always has done, concave glasses.

In the accompanying Fig. the globe of the eye is seen to be elongated. The continuous dark lines, *g g*,

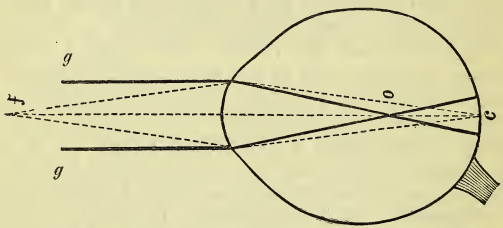


Fig. 23.—Diagram of the Course of the Rays in a Myopic Eye.

represent parallel rays, and these, by reason of the length of the eye, are brought to a focus at *o*, and, decussating, form a blurred image on the retina. In order to see an object distinctly, the patient brings it nearer to the eye, as to *f*, which we may regard as his far point. The diverging rays which then proceed from it he can, without effort, focus on his retina at *c*, as indicated by the dotted lines. If he bring it nearer than *f*, he can still focus it clearly, providing he exerts his accommodation, till at last he reaches a point (his near point) beyond which he cannot focus the rays by any effort of his accommodation. In high degrees of myopia, either one eye alone is used, or the power of converging the eyes must be very great, for the object has to be approximated very closely to the eye, and fatigue is soon experienced.

Hypermetropia.—Long-sightedness. In hypermetropia the eye is flattened. The far point is

beyond infinite distance, if the term may be allowed. Rays of light emanating from all objects at a measurable distance are divergent. Those from objects at an infinite distance are parallel. Neither of these can be focussed on the retina by a hypermetropic eye. At rest, the diverging rays emanating from a near object must be rendered convergent by a convex lens, or by a more or less energetic contraction of the

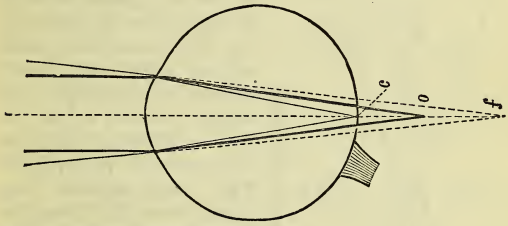


Fig. 24.—Diagram of the Course of the Rays in a Hypermetropic Eye.

ciliary muscle. This muscle soon becomes fatigued, and then exhausted, and near objects can no longer be seen.

The conditions are shown in Fig. 24. It is here seen that parallel rays, indicated by the dark continuous lines, are not brought to a focus on the retina, but behind it, at *o*. Objects that emit parallel rays of light, as, for example, the moon, are not seen distinctly by the hypermetropic person when his eyes are at rest; but, if he exerts his accommodation, and renders his lens thicker, then he brings up the focus from *o* to *c*, and he sees the object distinctly; but he is in worse case with near objects. Rays proceeding from near objects are divergent, and hence are only brought to a focus, as indicated by the dotted lines, far behind the retina, as at *f*. By an extraordinary exertion of the ciliary muscle, the suspensory ligament

may be for a short time so relaxed, and the lens rendered thicker, that the focus is brought up from *f* to *o*; but the effort cannot be long sustained, the muscle relaxes, and all near objects become indistinct. The appropriate means of relief consist in the application of glasses of such strength, that, as shown by the thin lines, they cause rays of light from distant objects to converge sufficiently to unite on the retina without any effort on the part of the subject. The long-sighted man should wear the strongest glasses with which he can see distant objects well.

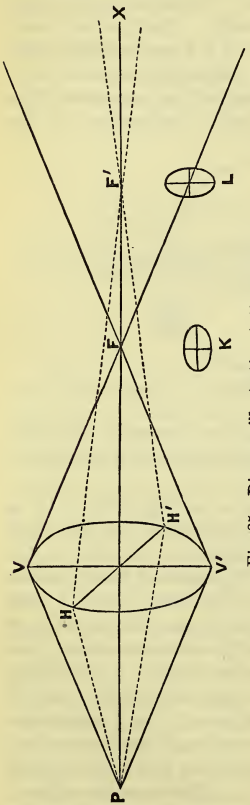


Fig. 25.—Diagram illustrating Astigmatism.

Astigmatism.—This is so common a defect of the eye that it may almost be regarded as the normal condition. When considerable, it occasions great impairment of vision. It consists in an inequality of the refraction in the different meridians of the eye, and is usually caused by the curvature of the cornea being different in the two meridians. The curvature in the vertical meridian is usually sharper than in the horizontal. Its refractive power is therefore greater

in the vertical than in the horizontal meridian. Under these circumstances, the eye is unable to bring the image of a point of light to a focus on the retina. If P (Fig. 25) be the point of light, and V V′ represents the vertical meridian or sharper curve of the cornea in a case of simple myopic astigmatism, and H H′ the horizontal meridian, the rays P V, P V′ will be brought to a focus at F; whilst those falling in the horizontal meridian, P H, P H′, will not be brought to a focus so soon, but at a farther point, F′. Hence, at F the image of the point will be horizontally elongated, as at K, by reason of the rays V F, V′ F having come to a focus, whilst the horizontal rays P H P H′ have not yet met. At F, on the contrary, the image will be vertically elongated, as at L, because the vertical rays have come to a focus and crossed.

When, in such an eye, a series of lines, radiating from a centre, is placed before it, that line will be seen most distinctly which is parallel to the astigmatic meridian, which would here be the vertical one; for the image of a vertical line will be formed by the superposition of small vertical lines. These overlap each other in the astigmatic meridian, and make the line somewhat longer indeed and blurred at the ends, which is not noticed, but blacker and more distinct; whilst the line at right-angles to the astigmatic meridian is blurred and confused, being formed by the apposition of a series of vertical lines (Fig. 26).

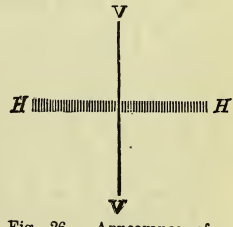


Fig. 26. — Appearance of a Cross in a case of Simple Myopic Astigmatism, vertical Curvature sharpest.

The defect is corrected in ophthalmic practice by cylindrical glasses, the curvature of these being nil in one axis, and more or less considerable in the opposite

axis, in correspondence with the degree of astigmatism that has to be corrected.

Irradiation.—By this term is understood the tendency of a brightly illuminated surface to encroach upon an adjoining black surface, as a result of imperfect accommodation. A black letter upon a white ground, therefore, appears smaller than it really is, whilst a white letter on a black ground appears larger. When accommodation is perfect, irradiation is not observed.

Entoptic phenomena.—This term is applied to subjective visual sensations, sensations that are perceived by the eye itself. The most important of these are Purkinje's figures, phosphenes, and muscæ volitantes, of which there are several varieties. Thus, if the clear blue sky be looked at for some time, a number of bright spots will be seen moving to and fro, like the sparks in tinder, or like the movements of the small black water beetle named Gyrinus. These are the blood corpuscles moving in the retinal capillaries. Another form is that of strings of transparent pearl-like bodies, which are the *débris* of cells in the vitreous. These are not very persistent, and are of much less importance than the presence of one or more black spots, sometimes with a tail of semi-transparent cell-like bodies, or a chain of globules attached to it or them. These move with the eye, and continue to move for some time after the eye has been brought to rest. They are usually considered to be masses of pigment, which have separated from the choroid or ciliary processes, and have entered the space between the lens and the vitreous, or have become entangled in the vitreous. They may also be exudation masses, or small masses of effused blood. They are of common occurrence in cases of hypermetropia, and appear to be caused by the subject pressing and rubbing the eye after exertion. Muco-lachrymal

figures may be brought into view by looking through a minute hole in a card at the flame of a lamp. These move with the eyelids.

Purkinje's figures.—If, after the pupil has been widely dilated by remaining in a dark room for some time, a candle be waved before it in various directions, the outlines of the vessels will be seen. These, as is well known, lie in the anterior layers of the retina, and their shadows are consequently thrown on the rods and cones which form the posterior layer of the retina, and are the light-perceiving elements.

Phosphenes.—When the eye is turned strongly inwards, and the finger is lightly pressed on the outer side of the globe as far back as possible, a phosphorescent-like luminous ring is seen on the side opposite to that on which the pressure is made. It is due to the mechanical irritation of the retina at the point pressed, which is projected outwards.

Purkinje's images.—When a ray of light falls on the eye it is in part reflected from the successive limiting planes of the different media, and before the invention of the ophthalmoscope much use was made of the images thus formed, and specially described by Purkinje, to determine the presence of cataract. If the pupil be large, or, better still, artificially dilated with atropine, and a candle with a steady flame be placed a little to one side of the subject, whilst the observer stands in front of him, three images of the candle will be seen: A large erect one, reflected from the convex surface of the cornea; a smaller erect one, from the anterior surface of the lens (both of these move with the candle if the position of this be altered); lastly, there is a still smaller image, which is inverted, and moves in the opposite direction to the candle; this is reflected from the posterior concave surface of the crystalline lens.

The presence of an opaque lens is rendered evident by the disappearance of the inverted image, which is formed by light that has passed through the lens to the posterior surface, and has been reflected from it. The non-appearance of the second or smaller erect image demonstrates that the pupil is obstructed by an exudate, or that there is turbidity of the aqueous humour, or cloudiness of the cornea, all of which interfere with its production.

Cause of erect vision. — The images of external objects formed on the retina are necessarily inverted, and it has been thought that we really see the world upside down; and attempts have been made to explain the mode in which visual sensations are made to harmonise with tactile, auditory, and other impressions. There is, however, no reason for believing that such antagonism between the senses exists. The rays coming from the lower part of the field of vision affect the rods and cones situated in the upper part of the retina, and those from above affect the lower ones; but it is easy to conceive that at the central extremity of the nerve fibres, the mind takes cognisance of the direction from which the rays have entered the eye, and refers them back to their normal source, or, as it is said, projects the image outwards. A good illustration of the "law of visible direction" is given by Leconte. If a pin-hole be made in a card, and the card be held at a distance of four or five inches before the right eye, with the left eye shut, and a pin-head be now brought very near to the open eye, so that it touches the lashes, and in the line of sight, a perfect *inverted* image of the pin-head will be seen in the pin-hole. If, instead of one, several pin-holes are made, an inverted image of the pin-head will be seen in each pin-hole. The explanation is as follows:—If the pin were farther away, say six inches or more, then light from the pin would be brought to

focal points, and produce an image on the retina, and this image being inverted would, by projection, be reinverted, and the pin would be seen in its real position. In the above experiment, however, the pin is much too near the retina to form an image. But nearness to the retinal screen, though unfavourable for producing an image, is most favourable for casting a sharp shadow, and whilst retinal images are inverted, retinal shadows are erect. The light streaming through the pin-hole into the eye casts an erect shadow of the pin-head on the retina. This shadow is projected outward into space, and, by the law of direction, is inverted in the act of projection, and therefore seen in this position in the pin-hole. It is further proved to be the outward projection of a retinal shadow by the fact that, by multiplying the pin-holes or sources of light, the shadows are multiplied, precisely as shadows of an object in a room are multiplied by multiplying the lights in the room.

Single vision with two eyes.—The two eyes act together, and when directed to any object, that object is seen single, because its image falls upon what are termed "corresponding" or "identical" points of the retina; if the images fall on any other points, double images will be formed.

The course of the fibres distributed to the retina.—The diagram here given (Fig. 26A) has been constructed by Charcot, partly from the results of experiment and partly on clinical grounds, to render the course of the fibres of the optic nerves intelligible. If we suppose the fibres of the optic nerves to arise from two centres of the cerebral cortex on the right and left side RCC or LCC, some of these fibres *a b'* course down the optic tract of their own side, pass to the opposite side in the chiasma OC, and are distributed to the inner or nasal side of each eye I I. other fibres *a'b* arising from the same cerebral centres

cross to the opposite side in the corpora quadrigemina CQ, and proceeding along the opposite optic tract and optic nerve, are distributed to the outer part of each eye. Owing to the partial decussation in the chiasma,

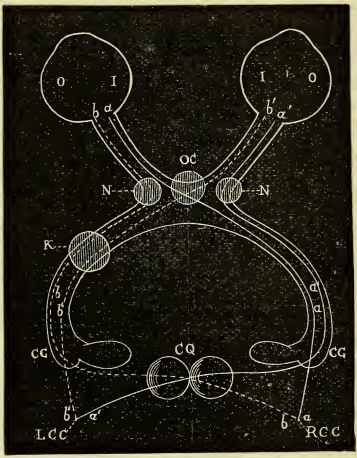


Fig. 26A.

I Inner side of the eye; O, outer side of the eye; C, commissure; N, outer part of commissure; K, circle placed on optic tract; CGCG, corpora geniculata of optic thalamus; CQ, corpora quadrigemina; RCC, right cerebral optic centre; LCC, left cerebral optic centre; *a b*, fibres passing to left eye; *a′b′*, fibres passing to right eye.

the left optic tract *b b′* thus receives the fibres *b* from the outer or temporal half of the left retina, and others *b′* from the nasal half of the right, that is to say, contains fibres conducting impressions from the right half of each visual field. In the same way the right optic tract conducts impressions from the left half of each visual field. Owing to the second partial decussation in the corpora quadrigemina,

each cerebral centre receives all the fibres from one eye only; the left cerebral centre those from the right eye, and the left those from the left eye.

If the concave right retina were lifted bodily out of the eye, and superimposed upon the left retina, the "corresponding points" of the two retinæ would be in contact; the outer half of the right retina would cover the inner half of the left retina, and the inner half of the right would cover the outer part of the left retina. The images of all objects falling on the outer side of the right retina and the inner side of the left retina, or *vice versâ*, fall therefore on corresponding points, and are seen single. The area of space, rays proceeding from any part of which fall on corresponding points, and in which, therefore, all objects appear single, is termed the *horopter*. The precise form of the horopter is unknown. The difficulty of determining it lies in the difficulty of recognising double images when they are formed at some distance from the macula lutea.

Rhodopsin or **visual purple.**—The structure of the retina is given in detail in Klein's "Histology," and it is there stated that the outer segments of the rods, but not of the cones, contain in the fresh and living state a peculiar diffused purplish colouring matter, named rhodopsin. It is not present in the rods near the ora serrata. It is non-diffusible, insoluble in solutions of urea, or in melted paraffin. It is soluble in solutions of the biliary salts. It is easily destroyed by chlorine, nitrous acid, ether, chloroform, aldehyde, and oil of turpentine; but it resists the action of ozone, permanganate of potash, ammonia, and sodium chloride. When exposed to the light of day, it rapidly bleaches. Exposure to a temperature of 50° C. in the dark causes bleaching to begin, becoming very rapid as the temperature rises to 70° C. When, after being bleached, the retina is kept in

darkness, it is capable of regaining its colour if preserved in contact with its natural background.

Optograms.—The action of light upon rhodopsin was first demonstrated by Kühne in the following experiment : In the opaque wooden wall of a dark chamber he bored a hole, which he covered with a circular diaphragm 5 mm. in diameter. The hole looked into a second chamber, in which was only one ground-glass pane, on which the bright noon-day light fell. In order to see how this bright pane, which was about 5·77 metres from the wooden wall just mentioned, came out as an image in the rabbit's eye, he first of all hung over it an intensely coloured chrome-yellow tissue paper, and arranged an eye in the following way : an Albino rabbit, after being kept fifteen minutes in the dark, was decapitated. One eye was removed from the head under the monochromatic light of a sodium light, was somewhat cleared at its posterior surface, and fastened on to the edge of a cork by means of needles run through the remains of the conjunctiva. Thus prepared, the eye was placed in position in the dark chamber, with the cornea pressing softly against the diaphragm. The image was visible on the sclerotic on one side of the optic nerve, a portion of which had been left attached to the eye, and so far beneath the point of entrance of the nerve into the bulb that he was sure that it fell on the more deeply coloured division of the retina, and could readily mark its place in the appropriate quadrant. Thereupon the yellow curtain was removed from the pane, and the eye, after five minutes' exposure, was taken away, divided along the equator, and examined in feeble gaslight. Being unable to recognise any image on it, he brought the preparation out into diffused daylight, and showed it to several witnesses. There was evident on the retina a most distinct brighter diffused spot, the

small dimensions of which corresponded to those of the image he had previously seen, and the position of which made him already sure that it was the optogram. All the observers recognised the spot as being in the same place. The eye was removed from its support, and for his own satisfaction he tried to find on the sclerotic from behind the previously observed position of the image. In this he was completely successful, owing to the help given by the small remains of the ocular muscles, the position of which, in reference to the position of the image, had previously been observed, and he was able to thrust a needle through from behind, which went straight through the pale spot; still the image was not precise, and it was only in after-experiments, in which he used a 4 per cent. solution of potash-alum to harden the retina and fix the retinal purple, that the details of the image thrown on the retina, as the cross-bars of a window, became clearly visible.

The pigmented cells forming the outermost layer of the retina send filiform prolongations between the rods and cones as far as to the external limiting membrane, and Kühne has demonstrated that under the influence of light, the crystalline particles of black pigment extend into these cells, processes, and surround the rods and cones, by which means they are isolated, and protected from all light, except that which travels directly along their axis. In darkness the pigment recedes again into the bodies of the cells.

Binocular vision.—The importance of binocular vision is shown by the difficulty that is experienced in threading a needle, or in pouring wine into a glass, with one eye closed; and this is due to the circumstance that pictures on the retina convey to the mind only the notion of a plane surface. The mode in which the mind estimates distance with

one eye alone is by variations of light and shade, by degree of exertion of the accommodation to obtain distinct vision, by experience of form and size, by parallactic motion, and by probability; but when both eyes are used, an impression of solidity is at once obtained; a stereoscope effect is produced, and the relative position of objects is much more accurately estimated. If a card with a name be held edgewise before the nose, it will be found that the name may be read with one eye, whilst the back of the card will be seen by the other. It is the combination of two dissimilar images that enables us to judge that the card has a certain depth, and that a pillar is round and not flat. The stereoscope itself is only an instrument by which two plane figures drawn or photographed, as seen with the two eyes, are superimposed upon each other, and which immediately give the effect of solidity; the objects in the foreground standing out in strong relief against those in the middle distance and background.

Decomposition of light.—The white light of the sun is composed of *colorific* rays of various degrees of refrangibility, which are therefore separated from each other when they are made to traverse a prism. The red rays are least refrangible, and then in succession the orange, yellow, green, blue, indigo, and violet rays, which are the most refrangible. The rapidity of the undulations is very great; the red ray vibrates 481 billions of times in a second; the violet 764 billions. There are other rays in the solar spectrum besides those of light. There are rays, which are invisible indeed, but which act strongly on the thermometer (*calorific* rays) which are less refrangible than the red; and there are rays which are more refrangible than the violet, which are also invisible, but which are recognised by their powerful chemical action, and are sometimes called "*actinic*," or "ultra violet," rays.

Attempts have been made to distinguish the several coloured rays of the solar spectrum into pure colours and mixed colours. At one time it was thought that the fundamental colours were red, yellow, and blue; orange was believed to result from the blending of red and yellow; green from the mixture of yellow and blue. More recently the fundamental colours have been held to be red, green, and violet; whilst Hering reverts to the view long ago held by Leonardo da Vinci, that the primary colours are red, yellow, green, and blue.

Complementary colours. — Complementary colours are those which, when mingled, theoretically produce white light. Examples of complementary colours are said to be found in red and bluish-green; orange and light blue, yellow and indigo, greenish-yellow and violet, green and purple, which last is a compound colour; but none of these compounds really produce the impression of white light on the eye; they are merely antagonistic colours.

Perception of colours. — On the theory of Young it is believed that the retina possesses three kinds of elements, the stimulation of which gives respectively the sensation of red, green, and violet rays. White light excites all the elements equally; but if homogeneous or monochromatic light be received upon the retina, then each of the three kinds of fibres is stimulated, with an intensity which varies with the length of the waves. Thus: red light, which has waves of the greatest length, stimulates the red elements strongly, the green more feebly, and the violet elements slightly, and the sensation experienced is red. Green, which has waves of intermediate length, stimulates the red and the violet elements feebly, but the green elements strongly, and the sensation perceived is green; and so with violet, which has waves of the shortest length, and which acts as a powerful

stimulus to the violet elements of the retina, but scarcely affects the green and red elements.

The three curves culminating at R, G*r*, and V (Fig. 27), show that the retinal impression of these colours in greatest intensity are produced by their own special colour with slight admixtures of the other special colours.

The intermediate colours are, of course, produced by the mixture of sensations; thus, the sensation of yellow is caused by the nearly equal stimulation of the

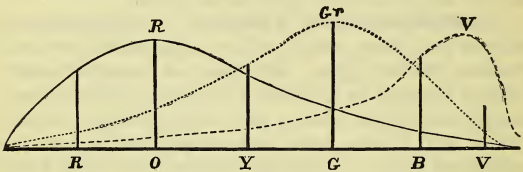


Fig. 27.—Showing the Distribution of the Primary Colours in the Spectrum. R, red; O, orange; Y, yellow; G, green; B, blue; V, violet.

red and green perceiving elements with slight stimulation of the violet, and so on.

A very different view has been advanced by Hering, who considers that colour is the mental perception of the changes taking place in the visual substance, which, under the influence of light, is constantly undergoing a double process of disintegration and reparation. Perception of white light is coincident with disintegration; of blackness or darkness, with redintegration; and the degrees of white and black depend on the activity of the processes of disintegration or repair. Besides white and black there are two other pairs of antagonistic colours, the perception of which is similarly dependent on processes of construction or destruction. Red and yellow result from destructive or disintegrating processes; green and blue, from constructive or redintegrating processes. The

visual substance, rhodopsin, or material, by whatever name it is called, which is sensitive to colour, is thus supposed to be composed of three constituents; the black and white perceiving, the blue-yellow, and the red-green perceiving substance; all luminous rays produce disintegration of the black-white perceiving substance, though the different rays act with different degrees of energy upon it. There are only certain rays, however, which act as decomposers of the blue-yellow or red-green constituent, whilst other rays act as constructive agents, and others again have little or no action.

Colour blindness.—About three or four per cent. of men, and a less proportion of women, fail to distinguish certain colours. The most common defect is the inability to distinguish between red and green. The peculiar character of red rays is not perceived; the subject is unable to recognise, otherwise than by their form, the cherries from the leaves of a cherry tree. This defect (red-blindness, as it may be called) is supposed, on Young's theory, to be due to the absence of the red-perceiving elements of the retina; and, on the theory of Hering, to the absence of the red-green constituent of the colour perceiving substance. In the violet blind, the yellow-blue constituent is absent.

There are degrees of colour blindness; in some, whilst saturated colours can be readily recognised, the different shades of the same colour fail to be distinguished. This is termed partial colour blindness. In complete colour blindness only shades of black and white can be perceived, and both the yellow-blue and red-green constituents of the visual substance are absent.

Positive and negative after-images.—If the retina be exposed to a very bright light, which is then suddenly extinguished, there remains for a short

time an impression of the same colour, as though the retinal elements still continued to vibrate in response to the same stimulus. This is the *positive after-image.* After a little while, however, the positive image is replaced by a *negative after-image,* in which the bright parts of the real image and of the positive after-image, become dark, and the dark parts light. The appearances in question are well seen on looking intently at the sky through cross-barred or cottage windows for a minute or two, and then closing the eyes; the bars, at first dark on a light ground, soon become light on a dark ground.

When the object is of a bright colour the negative after-image presents the complementary colour, and the tint of the complementary image becomes most pronounced when the eye is turned upon a uniformly grey surface. The experiment is made use of in a well-known advertisement, in which the name of the firm is printed in vermillion, with a blank space of equal dimensions below, to which the observer is directed to look, after gazing steadily at the name for a few seconds. The name appears in the blank of a vivid green colour. Many fail to see the negative after-image, which is due to the fact that they have not kept their eyes fixed on one spot, but have allowed them to wander.

The after-image of a bright white object passes through a series of coloured phases, which is explained by Helmholtz on the supposition that fatigue supervenes more readily for one energy than for another. When about to disappear, or even after total disappearance, a slight movement of the eye or head brings after-images more or less prominently into view again.

Coloured shadows.—If the light of day be admitted into an otherwise darkened room through two apertures, one of which is free, whilst into the

other a piece of coloured glass is inserted, and a pencil is held at a convenient distance in front of a white screen, two shadows of the pencil will be thrown on the screen, the depth of which may be equalised by a diaphragm. It will then be found that the tint of the shadows will present complementary tints, so that if a piece of red glass be inserted into one of the apertures, the shadow of the pencil thrown by the light entering the free aperture, being illuminated by the red light entering by the other aperture, will appear of a reddish colour, whilst that thrown by the red aperture will appear of a complementary tint, that is to say, of a greenish colour. So if one of the sources of light be a candle, and the other the sky, the shadow of the pencil thrown by the candle will be yellowish red, and that of the sky will, by contrast, appear blue.

Muscles and movements of the eye.—Each eye is moved by six muscles, which are arranged in pairs, each pair rotating the eye in opposite directions round a definite axis. To facilitate the comprehension of their action, it is also useful to remember that a vertical line halving the cornea is termed the *vertical meridian.* The names of the muscles and their actions are :

{ Internal rectus, which rotates the eye inwards.
{ External rectus, which rotates the eye outwards.

In the case of these two muscles the axis of rotation is vertical. When they act, although the globe is rolled inwards, the vertical meridian is not altered in direction, but remains vertical.

{ Superior rectus, which rotates the eye upwards.
{ Inferior rectus, which rotates the eye downwards.

In the case of these two muscles, the axis of rotation is horizontal, but slightly oblique from

nose to temple. (*See* Fig. 28.) The superior rectus acting alone, not only turns the eye upwards, but causes the vertical meridian to incline inwards, and to obtain a true rotation upwards the inferior oblique is also brought into play, which inclines the meridian outwards.

In the case of the inferior rectus the same is observed. The inferior rectus not only rotates the

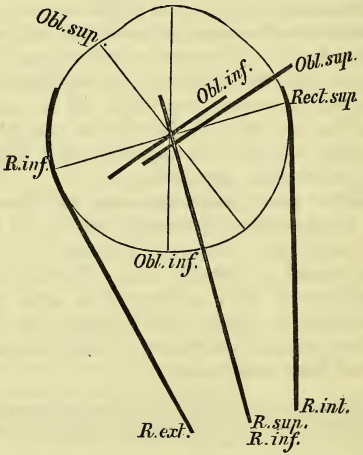


Fig. 28.—Diagram showing relative Attachments of the Ocular Muscles. The thin lines show the axes of rotation.

eye downwards, but inclines the vertical meridian outwards, and this is corrected by the coincident action of the superior oblique, which inclines the vertical meridian inwards.

{ Superior oblique—rotates the eye downwards and outwards.
{ Inferior oblique—rotates the eye upwards and outwards.

The axis of rotation of the oblique muscles lies in the plane of the horizontal diameter of the globe, but forms an angle of 60° with the transverse axis. The superior oblique inclines the vertical meridian inwards. The inferior oblique inclines the vertical meridian outwards. (*See* Fig. 28.)

Lacrimal apparatus.—The secretion of the lacrimal gland, named *tears*, is a protective fluid. It is discharged into the conjunctival sac at its upper and outer part, and serves to wash away any foreign body that may have entered between the lids and become adherent to the conjunctiva. The secretion is very thin and watery, containing nearly 99 parts of water and one part per cent. of albumin, mucin, and salts, and may be excited through the optic nerve by exposure of the eye to a bright light, through the branches of the fifth nerve distributed to the conjunctiva and nose, and by mental excitement. The centre is probably in the pons or medulla oblongata. The motor nerves are the lacrimal of the fifth and the small temporo-malar nerve. After having traversed the surface of the globe of the eye, the tears enter the puncta, partly by capillary attraction and partly by the action of Horner's muscle and some fibres of the orbicularis, which on contracting dilate the lacrimal sac, and produce a tendency to a vacuum, which the tears rush in to fill. The continued action of the same muscle compresses the sac and forces the fluid down the nasal duct, regurgitation being prevented by several but irregularly placed folds. The inspiratory act also promotes the passage of tears through the duct. The surface of the globe is further kept moist by the mucous secretion of the inner surface of the eyelids. The lids are prevented from adhering during sleep by the secretion of the Meibomian glands, which open on the free margin of the lids behind the attachment of the cilia.

THE SENSE OF HEARING.

This sense is due to the excitation of the eighth or auditory nerve. The organ of hearing is divided into three parts—the external ear, including the auricle and the meatus; the middle ear, or tympanum; and the internal ear, or labyrinth. The external ear has for its function the collection and transmission of sounds to the membrana tympani. The importance of the auricle is shown by its constant motion in animals like the horse, cat, and hare. In man its function is subsidiary; it has become flattened, the muscles are atrophied, and its movements are scarcely perceptible. If the inequalities of one auricle be filled with wax, the perception of sounds is not impaired, as compared with the opposite ear, when the meatus is directed towards the source of the sound; but in all other positions it is much diminished.

The **membrana tympani**, or **drum of the ear.**—This is a membrane composed of a basis of fibrous tissue, with a prolongation of the external skin on the one side, and of the mucous membrane of the tympanic cavity on the other. It is concave when viewed externally, is not very tightly stretched, and is inelastic. The handle of the malleus is firmly attached to it. The planes of the two tympani converge anteriorly, and if prolonged would meet at an angle of about 130°. The tympanum vibrates to and fro as a whole with undulations of the air, and its vibrations are communicated directly to the ossicula auditûs, which not only conduct the vibration to the labyrinth, but act as dampers, and prevent after-impressions to a very material extent. The membrana tympani has no fundamental note of its own, but vibrates with nearly equal readiness to notes of very different pitch.

The **ossicula.**—These, consisting of the malleus,

incus, and stapes, conduct the vibrations of the air from the membrana tympani to the labyrinth, through the foot of the stapes, which closes the foramen ovale.

The handle of the malleus penetrates between the lamellæ of the membrana tympani as far as to the umbo, and is connected by means of a neck with the rounded caput; the neck is embraced by a ligament named by Helmholtz the axis ligament, which is attached to a process of bone on the outer wall of the tympanic cavity, and forms the axis around which the malleus can swing to and fro. The head of the malleus articulates by a convex surface with the concave articulating surface of the incus, and the incus presents two processes, of which the longer one articulates with the little process at the apex of the arch of the stapes. The foot-piece of the stapes fits into the foramen ovale, and closes it, occluding the communication between the tympanic cavity and the labyrinth. A superior ligament limits the movements of the malleus and incus outwards, and prevents the foot of the stapes from being drawn out of its frame; and a ligament also connects the short process of the incus to the posterior wall of the tympanum.

When, in consequence of a sound wave impinging upon the membrana tympani, it is driven inwards, as indicated by the lowermost arrow (Fig. 28A), the handle of the malleus moves with it; but as the malleus rotates on the axis ligament the head will move in the opposite direction, and with it the closely articulated incus. The long process of the latter bone will, on the other hand, like the handle of the malleus, move inwards, and consequently press the foot of the stapes into the fenestra ovalis. There is a special arrangement of small spurs of bone at the malleo-incudal joint, which, whilst it compels the incus to move with the head of the malleus outwards, yet, if the membrana tympani with the handle of the malleus is by any means

pressed outwards, it unlocks, permitting the articular surfaces of the malleus and incus to separate, and preventing the stapes from being dragged from the fenestra ovalis. The ossicula constitute a lever with two arms of unequal length, the longer being the handle of the malleus, the shorter the head of the malleus, with its appendages, the incus and stapes. The length of the handle of the malleus to the axis ligament is about one and a half times greater than that of the rest of the malleus, the latter, therefore, will only make an excursion of about two-thirds the extent of the movement of the handle and membrana tympani. On the other hand, the force which the head of the malleus, with the incus and stapes, exerts is inversely about one and a half times greater than that of the handle of the malleus. Since, further, the membrana tympani is about twenty times larger than the membrane of the fenestra ovalis, and the force of the vibration of the membrana tympani is therefore concentrated upon a twenty times smaller membrane, the excursion of the membrana tympani, due to the movement of the ossicula, is converted into a movement of the membrane of the fenestra ovalis of much smaller amplitude, but of $1\frac{1}{2} \times 20$ or 30 times greater force. The vibrations of the air striking the membrana tympani, which

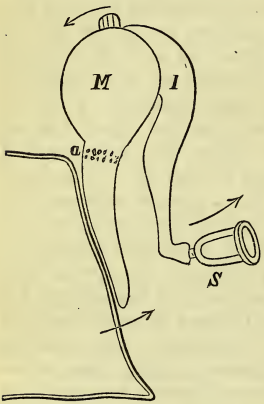


Fig. 28A.—Mechanism of the Ossicula Auditûs.

M, Malleus; I, incus; S, stapes; *a*, axis ligament.

have great amplitude but little force, are consequently converted by the lever system of this ossicula into a movement of small amplitude but considerable force, and therefore conduct the movement as perfectly as possible to the fluid of the labyrinth. By means of the ossicula, the muscles of the tympanum are able to modify the tension of the membrana tympani. The extent of movement impressed on the foot of the stapes by vibrations of the membrana tympani is very small, and has been estimated at 0·07 mm. The tensor tympani muscle stretches the membrana tympani by pulling the malleus inwards, and renders it capable of vibrating with acuter sounds.

The **Eustachian tube.**—The Eustachian tube permits the air in the tympanic cavity to be renewed, and the secretion of its mucous membrane to escape. The aperture of the tube is usually closed, but it is opened at the moment of swallowing, by the action of the fibres of the *dilatator tubæ*.

Function of the semicircular canals.—These canals partly supply information in regard to the direction of sounds and partly aid in maintaining the equipoise of the body. Their division does not appear to interfere materially with the perception of sounds, but induces very peculiar movements either of the head alone, or of the head and body. Thus, section of the horizontal canal in a pigeon causes it to turn its head alternately to right and left for months together. Lesion of the posterior vertical canal occasions nodding movements, so that the animals often either fall backwards or forwards. Lesion of the superior anterior canal also leads to vertical movements of the head; and it is believed by some that the position of the head is recognised by the pressure exerted by the endolymph upon one or other of the ampullæ. It will be observed that the three semicircular canals correspond to the three sides of a cube, and that

consequently in whichever direction sounds are propagated to the ear, they will affect one of the canals more readily than the others.

Function of the labyrinth.— The peculiar arrangement of the arches of Corti naturally led to the supposition that they acted like the successive wires of a piano, and vibrated in unison with the sounds affecting them from without; and it is only necessary to imagine that each arch is in connection with a nerve fibre, which is excited by its vibration, in order to understand how sounds of various pitch, intensity, and timbre come to be recognised. But since the arches of Corti are absent in birds, which must undoubtedly have very clear perceptions of musical sound, some other part must be looked on as fulfilling this function; and those which seem most likely are either the radial fibres of the membrana basilaris, on which the organ of Corti rests, and which are shortest in the first turn of the cochlea, and become longer towards the cupola, or the hairs of the hair-cells, which are known to be of different length.

Sounds are divisible into musical and non-musical. Musical sounds result from aerial undulations, which reach the ear in a certain order and regularity. Non-musical sounds, or noises, consist of undulations which have no periodic relation to each other, and reach the ear irregularly. The undulations strike the drum of the ear, are conducted chiefly by the chain of bones, but partly by the air contained in the tympanum, to the vestibule, semicircular canals, and cochlea, and are supposed to set the auditory hairs into vibration. Their vibration excites the extremities of the auditory nerve, and the impression being conducted to the auditory centre, produces there the sensation of sound.

The **interval of two notes.**—This may be expressed by a fraction, representing the proportion

the vibrations producing the two notes bear to each other. Thus, if one note is caused by 300 vibrations per second and another by 200, the proportion of the two is $\frac{300}{200}$, or $\frac{3}{2}$. Certain intervals are represented by comparatively simple ratios; and these the ear receives most readily, and are the most agreeable to it. They are those which are ordinarily emitted by the human voice. The simplest proportion is that termed the octave, in which the ratio is $\frac{1}{2}$. The higher note is here produced by double the number of vibrations by which the lower note is formed. The following table gives the relations of the chief simple intervals which are less than an octave.

Intervals.	Ratio.	Number of Vibrations of the Higher Note.	Number of Vibrations of the Lower Note.
Fifth . .	2 : 3	3	2
Fourth . .	3 : 4	4	3
Major third .	4 : 5	5	4
Minor third .	5 : 6	6	5
Minor sixth .	5 : 8	8	5
Major sixth .	3 : 5	5	3

The gamut is produced by preserving the more simple intervals, as the fifth, fourth, and third, and intercalating in the intervals of an octave a series of notes separated from each other by definite intervals. The notes of the gamut are seven in number, and their vibrations bear the following ratio to the vibrations of the fundamental note, or *tonic do.*

do	re	mi	fa	sol	la	si	do.
1	$\frac{9}{8}$	$\frac{5}{4}$	$\frac{4}{3}$	$\frac{3}{2}$	$\frac{5}{3}$	$\frac{15}{8}$	2

This is called the major gamut.

The minor gamut is also composed of seven notes, but in these the ratios of the vibrations between

themselves and to each other differ from those of the major gamut. They are as follows :—

do	re	mi♭	fa	sol	la♭	si♭	do.
1	$\frac{9}{8}$	$\frac{6}{5}$	$\frac{4}{3}$	$\frac{3}{2}$	$\frac{8}{5}$	$\frac{9}{5}$	2

There are other forms of the minor gamut, but this is the earliest and perhaps the most important of them.

The tonic of the gamut, whether major or minor, may be placed on any note indifferently, but the ratio of the vibrations in the successive notes in the major and minor keys do not correspond.

Dissonance.—Beats.—As long as sounds have a certain simple relation to each other, so that one is to the other as 1 : 2, 1 : 3, 1 : 4, and the higher note makes two, three, or four vibrations to each vibration of the lower note, harmony results; but if the relation of the higher note to the lower is not in the ratio of the multiple to the single, interferences must occur, and dissonance result. Thus, if one sound is produced by 33 vibrations per second and another by 34, the waves of the one must advance upon those of the other, till the crest of one undulation is exactly opposed to the depression of another. A distinct beat is then heard, which in this case would occur once in the second, and would recur at regular intervals of a second. Such isolated beats are frequently heard, and are distressing to a musical ear; but if the difference be greater, the beats of course recur with greater frequency, and dissonance is produced of so marked a character as to be perceptible to the most unmusical person.

Pitch of a sound.—The pitch of a sound depends on the number of vibrations in a given time. The greater the number of vibrations, the higher is the pitch. The perception of notes of successively higher pitch by the ear corresponds therefore with the perception of the succession of colours by the retina;

the difference between them lies in the rapidity of the vibrations, which in the case of light are counted by millions of millions, whilst in the case of sound they are at most only a few thousand in the second. The greatest number of sonorous vibrations that can be perceived is rather less than 41,000 per second, though few can hear sounds produced by more than 35,000 per second; the lowest that will give the sensation of a musical sound is about 16. Above the former number, no sound is perceived; below the latter, only a succession of beats, or puffs, when the instrument used is a wind instrument. A whistle has been constructed which, by being rendered shorter, can be made to yield shriller and shriller notes. If such a whistle be sounded in a mixed audience, it will be found that as the note is made sharper, the ears of a certain number of persons become incapable of responding to the vibrations, and they are perfectly deaf to them; whilst others are still capable of distinctly recognising them. Contraction of the tensor tympani muscle enables sounds of about 4,000 vibrations higher than normal to be perceived. In the same way, the cry of the bat, the squeak of the mouse, or the sound made by the cricket, are inaudible to many who have otherwise fairly good ears. Fineness of hearing, or the possession of a "good ear," signifies that minute differences in the pitch of two notes, produced by a nearly equal number of vibrations, can be perceived.

Timbre of a note.—The timbre of a note is the peculiar difference which enables even an ordinary ear to say whether a particular note is produced by a piano, a violin, a flute, or an organ. It depends on the number and nature of the harmonics which accompany nearly all musical sounds, and which may be rendered evident, either by resonators, which are large hollow vessels that respond to particular notes

strongly, and less or not at all to all others; or by examining the vibrations of a series of stretched cords in the neighbourhood of the note the timbre of which is required to be determined. Thus, if the wires of a piano are carefully examined whilst any particular note is sung by the human voice, or elicited by the bow from a violin, it will be found that not only the wire that is in unison with the note sung or played vibrates, but that several other wires are also thrown into vibration. These are harmonics or partial tones, thirds and fifths, which respond to corresponding vibrations in the vocal cords or in the cords of the violin, and it is the existence of these harmonics, overtones, or partial tones, that enable the difference between two instruments or their timbre, to be recognised.

Duration of the auditory sensations.—It has been ascertained by experiment that the human ear is capable of recognising as distinct beats 133 beats in a second, but beyond this number the successive impulses fuse into one, and the sound becomes continuous. Occasionally after-sounds are perceived, but as a rule the persistence of the individual sounds is very short. The recognition of differences between two notes varies greatly in different persons. Thus, some are scarcely disturbed by a sound which is half a note flat or sharp, whilst to others the difference produces a sensation that is akin to pain; and it is said that practised musicians will distinguish between notes the difference of which is not greater than 1 in 1,000. The A of musicians in Germany has 440 vibrations per second; in France, 435.

VOICE AND SPEECH.

Voice or vocal sounds are produced by most mammals. Speech is peculiar to man. Voice is produced by the vibrations of the inferior vocal cords. Speech

consists of the same vibrations, with modifications induced by varying size of the oral cavity, and varying position of the tongue and lips.

The **glottis** is the opening between the vocal cords. During ordinary respiration, and when no sounds are emitted, it is of triangular form, the apex being in front, and the base behind. The margins are formed by the *chordæ vocales*, or thyro-arytenoid ligaments. These are composed of extremely fine and delicate fibres of pure elastic tissue, connected on their outer surface with the thyro-arytenoid muscle. As soon as a vocal sound is required to be produced the cords are, by muscular action, rendered moderately tense, and their edges are brought into perfect parallelism. The passage of air through them with a certain degree of force, greater than that of ordinary expiration, throws them into vibration, and produces notes of various pitch and intensity, which may even be imitated in the dead subject by appropriate arrangements for driving air through them. The tighter the cords, the higher is the pitch of the note; the more slack the cords, the lower is the pitch. The vocal cords are stretched by the depression of the thyroid cartilage on the cricoid, through the agency of the crico-thyroid muscle; they are relaxed by the thyro-arytenoid muscles. The fissure of the glottis is widened posteriorly by the rotation outwards of the arytenoid cartilages caused by the crico-arytænoidei postici. It is narrowed by the simultaneous action of the crico-arytænoidei laterales, which rotate the arytenoid cartilages inwards, anteriorly, and by the arytenoid muscles posteriorly. The nerves implicated in the acts of vocalisation are the superior and inferior laryngeals. The former is the sensory, the latter the motor nerve. Lesion of the inferior laryngeal causes loss of voice from inability to bring the vocal cords into parallelism.

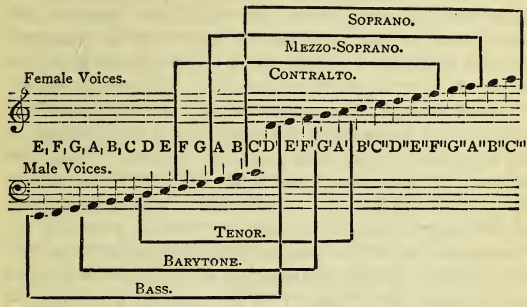
The **organs of voice and speech.**—Potter gives the following classification:

- Generating sound
 - Motor
 - Muscles of respiration.
 - *Ordinary.*
 - Diaphragm.
 - Intercostals.
 - Levators of ribs.
 - Scaleni.
 - *Extraordinary.*
 - Serrati maginni.
 - Latiss. dorsi.
 - Pectorals.
 - Thorax.
 - Lungs.
 - Bronchi.
 - Trachea.
 - Vibratile.
 - Larynx.
 - Vocal chords.
- Modifying sound
 - Resonant (vowel forming)
 - Vestibule of larynx.
 - Ventricles of larnyx.
 - Pharynx.
 - Oral cavity.
 - Nasal cavity.
 - Frontal sinus.
 - Sphenoidal sinus.
 - Epiglottis
 - Velum palati.
 - Inferior maxilla.
 - Articulating (consonant forming)
 - Tongue.
 - Lips.
 - Velum palati.
 - Teeth.
 - Inferior maxilla.

Compass of the voice.—The ordinary compass of the voice includes about four octaves, viz., from E  to C‴  the lowest note being produced by 80 vibrations per second; the highest by 1,024. Individual voices are stated by Potter* to have descended to F,  while Catalani sang G‴  and Aguiari is said by Mozart to have risen to C⁗ 

* "Speech and its Defects." Lea, Prize Thesis. 1882.

The compass and classification of ordinary voices is thus given by the same authority :



Falsetto voice.—This is a different and a higher register than the ordinary or chest voice. The aperture of the glottis is wider, and the superior vocal cords are more widely separated from each other, than in the production of the ordinary voice. It is believed to be produced by the vibration of the edges only of the vocal cords, whilst these are in a state of greater tension than in chest notes. A falsetto note cannot be sustained as long as a chest note of the same pitch.

Vowel sounds.—Vowels are continuous voice sounds produced in the larynx, but the overtones of which are modified by the different forms assumed by the oral cavity. If the trachea is opened, voice ceases. The buccal cavity either forms a cavity of equal diameter throughout, or enlarges its anterior segment whilst it contracts the posterior. The former occurs with the vowels A (broad), O, and U; the latter for A short, E and I. The buccal cavity is of maximum size in pronouncing the vowel A, and is smallest with U. For all the vowels the orifices of the nasal cavities are

closed by the elevation of the velum palati, without which nasal sounds would be produced (Budge).

Consonants.—Consonants are produced by the emission of shorts puffs of air, which are thrown into vibrations as they traverse the narrowed air passages. Simple expiration reinforced by the mouth produces *h*, or when the lips are closed, and the current of air directed through the nose, *m* or *n*. In the case of the majority of consonants the opening for the passage of air is at first closed, then suddenly opened. Thus, the explosive consonants, *b* and *p*, are formed by the sudden opening of the lips; *d* and *t* by the sudden separation of the tongue from the palate or teeth; *g* and *k* by the separation of the tongue from the posterior part of the palate. Simple contraction and closure of the lips takes place for *f* and *v*; of the tongue for *s* and *l*; and of the palate for *ch*, and *s* pronounced in German, and *t*. Consonants produced by approximating the lips to each other or to the teeth are termed *labials;* those formed by approximating the tip of the tongue to the teeth or to the hard palate are *dentals*, or *palatals;* and those produced by approximating the root of the tongue to the soft palate are *gutturals.*

Potter gives the following tabular arrangement of the consonants according to their acoustic relation:

	Labials.	Dentals.	Gutturals.
Explosives	P.B	T. D	K G
Aspirates	F V	S,Z,L, Sh J. Th (hard & soft)	Ch Y (initial)
Resonants	M	N	Ng
Vibratives		R	R

Whispering consists in the movements required for articulate speech being effected whilst the vocal cords are not thrown into vibration.

Sense of touch.—The cutaneous nerves terminate in the skin, partly by free extremities, and partly in special organs, termed tactile corpuscles and Pacinian corpuscles. Several different sensations are perceived by the skin. There are sensations of touch, of pain, of space or position, of pressure, of tickling, of temperature, and of muscular effort. Whether each of these has its own special nerve-end apparatus, and its own channel of communication with the central nervous system, is still undetermined. The sensations of touch proper, or tactile sensations, are only perceived by the skin, and the mucous membranes near their orifices. No tactile sensations are aroused by the passage of ordinary bodies along the intestinal canal, or along any of the ducts connected with it; or if any are excited, they are sensations of pain. All tactile sensations are most distinctly felt when they affect the periphery of the nerves; and in order that any kind of sensation should be felt, it is necessary that the stimulus should be suddenly increased in intensity, and not increased slowly or gradually. There must also be a free circulation through the part. The action of cold in numbing a part is well known.

Sense of space.—The most sensitive part of the body is the tip of the tongue, which is capable of distinguishing that the points of a pair of compasses are separated when there is only an interval of 1·1 mm., or $\frac{1}{24}$th of an inch between them. The tip of the third phalanx of the fingers is nearly as sensitive. The skin of the lips distinguishes the two points when they are only about 4 mm. apart; the middle of the dorsum linguæ and the skin of the metacarpus of the thumb, when they are about 8 mm. apart; the skin over the malar bone, when they are about 20 mm. apart. The least sensitive parts are the lower part of the back, and the outer part of the thigh, where the points of the compasses may be applied at a distance from each

other of 2½ inches, and yet not be certainly differentiated as two. An instrument termed an *œsthesiometer* has been devised, in which the distance between two points can be accurately noted, and by means of which the relative acuteness of sensibility of different parts of the skin in any case can be readily ascertained. The simultaneous but unusual excitation of two parts of the skin by any object gives the impression of the presence of two bodies, as in the experiment of Aristotle, in which a marble is touched by the outer side of the second and the inner side of the first finger when these fingers are crossed, which gives the impression of two marbles. In experimenting on the sensibility of the skin for all varieties of sensation, it should be remembered that great improvement takes place after short practice, and that experiments should be repeated many times before any trustworthy conclusions can be drawn. Those who are blind, and who have therefore to depend largely on the sense of touch for guidance, acquire extraordinarily delicate and accurate powers of perception with the fingers, differences of form, size, character of surface, consistence, temperature, and other characters, being readily recognised that are quite inappreciable to those who possess good vision, without special education. Tactile sensibility is most acute at temperatures near that of the normal temperature, 38·6° C. The greater the common sensibility of any part, the more rapidly may a succession of shocks or pulsations succeed each other, and still be distinguished as separate impulses. On the points of the fingers, 1,500 shocks per second can be distinguished, and on the tip of the tongue even 10,000 shocks per second still produce a vibratory sensation.

Sense of pressure. — By this special form of tactile sensibility we recognise the degree of resistance presented by different bodies. Its acuteness is ascertained by placing weights of the same size but of

different amounts on the skin of various parts of the body, and endeavouring to estimate them. The parts which perceive the sense of touch most acutely are generally also those which have the keenest sense of pressure, but not always. The smallest weight which can be perceived is 0·002 gramme, which is recognised by the skin of the forehead, the temples, the back of the head, and the fore-arm. The pulp of the fingers can perceive a weight of 0·005 to 0·015; the chin, nose, and belly, 0·04 to 0·05 gramme; and the finger-nail, 1 gramme. The points of the fingers can distinguish that one weight is heavier than another when the proportion between the two is as 29 : 30, providing they are not very light or very heavy. Experiments have been made to determine what additional weight must be added to one gramme in order that it should be perceived, and it has been found that on the third phalanx of the fingers the addition of 0·499 gramme to 1 gramme is perceived. On the lower leg a whole gramme must be added, and on the back no less than 3·8 grammes. The judgment is materially influenced by the length of time that is allowed to elapse between the trials, and no trustworthy conclusions are drawn when a little more than a minute and a half have elapsed. Considerable pressure may be exerted without its being perceived, if it is uniform. Thus, when the hand is plunged into mercury, the increased pressure is only felt at the line corresponding with the surface of the fluid.

Sense of temperature.—The sensations of heat and of cold are relative, and dependent upon the temperature of the part of the body exposed. This may easily be shown by dipping one hand into hot water, the other into cold, and then both together into water of medium temperature. This will feel hot to the one hand, and cold to the other. The fingers are capable of perceiving differences in temperature

of about 0·2° C. It is much more easy to perceive slight differences of temperature when a large surface of the skin is exposed to them, than when only a finger or limited surface is acted on. The left hand is more sensitive than the right. Temperatures near those of freezing water and of 50° C. usually produce pain, but custom, as in other cases, enables both low and high temperatures to be borne with impunity that are under ordinary circumstances quite unbearable. The skin, when deprived of the epidermis, appears to be incapable of perceiving variations of temperature, both heat and cold causing the sensation of pain. The sensitiveness of the mucous membranes for variations of temperature is very dull, the ingestion of a tumbler of cold water into the stomach, or the injection of cold water into the rectum, scarcely giving the sensation of cold, or producing it only by withdrawing heat from the adjoining skin.

Pain.—Pain results from excessive stimulation of any sensory nerve, and may be excited by the violent application of all forms of stimuli, whether mechanical, chemical, thermic, electrical, or due to some alteration in the body itself, such, for example, as inflammation. Some nerves are much more acutely sensitive to pain than others. The fifth nerve stands pre-eminent in this respect, and acute neuralgia of the several branches of this nerve almost paralyses the sufferer, every movement being inhibited lest it should intensify the pang. The splanchnics are also highly sensitive nerves. The organs which, when inflamed, give rise to the most intense pain are those which are well supplied with nerves, and which have a dense unyielding fibrous investment, examples of which are found in the testes, in the ovary, and in the eye. Pain can be excited by violent stimulation of a nerve in any part of its course, but it is often referred to its peripheral extremity. Remarkable examples of this

are found in cases of amputation, in which irritation of a nerve at the line of section is referred to the distal part of the limb which has been removed.

Muscular sensibility.—The muscles, though they are not very sensitive organs to ordinary stimuli, yet, when contracted spasmodically, occasion severe pain. They ache when fatigued, and pain is felt when they are contused or cut. They also possess a certain sensibility, which enables us to tell not only whether they are in contraction, but to what degree they are contracted, and this has been distinguished as the "muscular sense" proper. Experiment seems to show that the acuteness of the muscular sense for the amount of exertion made is greater than that of the sense of pressure or resistance possessed by the skin, for, whereas the skin, as we shall see, can only distinguish between weights differing from each other in the proportion of 29 : 30, weights can be recognised as different when weighed in the hands which do not differ more than 39 : 40. Experiments of this kind can be best made by concealing the weights to be estimated in small bags, and endeavouring to form a correct judgment as to their respective weights. The muscular sense affords indications (1) of the energy of contraction of the muscle, (2) of the extent of contraction, (3) of the rapidity of the movement, (4) of the duration of movement, and, lastly, (5) of the position of the limbs and of the body. By some observers it is maintained that the occurrence and degree of contraction in a muscle is only known by the effort, or nervous expenditure, put forth to cause the muscle to contract; whilst others think we only become aware of the contraction of a muscle by the cutaneous or tactile sensations that are coincidently excited. In accordance with this, the heart and diaphragm, which only remotely affect the skin, have very feeble muscular sense. It is, however, now very generally admitted

that there are special nerve fibres charged with the office of ministering to the muscular sense. Section of the posterior roots of the nerves supplying the hind limbs in dogs produces much more disturbance in the movements of the animal than section of all the cutaneous nerves supplying the same limb.

Sense of taste.—The faculty of taste is localised in the tongue, especially at its posterior part, and in the lower part of the velum palati. The papillæ circumvallatæ possess special organs which are believed to be adapted for this purpose. (*See* Klein's "Histology," p. 193.) The nerves implicated are the glossopharyngeal, which is the proper nerve of taste, and supplies the posterior part and sides of the tongue with the circumvallate papillæ; the pterygo-palatine branches of the fifth pair, which supply the velum palati; and the lingual of the fifth, which is distributed to the tip of the tongue. The conditions necessary for the exercise of the sense of taste are that the object to be tasted should come into direct contact with the organ of taste, and consequently sapid substances must be in solution; secondly, that the nerves of taste should be specifically excited; lastly, attention and judgment.

There are four chief varieties of savours: sweets, bitters, acids, and salines. Sapid substances are more distinctly perceived and distinguished in proportion (1) to the extent of surface to which the substance is applied, (2) to the degree of concentration of the substance, (3) to the duration of the time that it is applied, (4) to the degree of practice, and (5) to the approximation of the temperature to the normal temperature of the body. Wine and tea tasters take a moderate quantity of the fluid into the mouth, and roll it over the tongue and cheeks so as to increase the surface to which it is applied. Some substances, as quinine, have a very persistent flavour, and it has been estimated that a solution of common salt must be

twenty times as strong to produce the same vividness of impression as quinine. The rapidity with which the gustatory impressions of different substances are perceived varies. Salt is tasted most quickly, being perceived 0·17 sec. after its application, whilst quinine requires 0·258 sec., and sweets and acids occupy an intermediate period. Many gustatory sensations are materially assisted by the sense of smell.

Sense of smell.—The organ of smell is situated in the upper part of the nose; a portion of the mucous membrane covering the upper and middle turbinals, and the septum nasi, being specially modified for this purpose. The nature of odorous emanations is not certainly known. They may consist of aerial undulations, or they may be minute particles of the odorous substance. In either case they are extremely delicate, air containing only a millionth part of hydrogen sulphide having a distinct odour, whilst a minute portion of musk will continue, without appreciable loss of weight, to render its presence perceptible in a large apartment for years. Odorous emanations are conducted to the nostrils by the air; and water or eau de Cologne, however strongly they may be impregnated with odorous substances, convey no impression of smell when they are made to fill the nostrils. The air must also be in motion, and to effect this a respiratory effort is made, by which a current is directed towards the upper part of the nasal cavities. The olfactory nerve is the nerve of smell, and through it we perceive aromatic, nauseating, and other odours. Attempts have been made to classify odours, without success; but after section of the olfactory nerves in animals, and in cases of disease in man, certain stimulating odours can still be perceived; and the retention of this power must be attributed to the sensibility of the mucous membrane generally, which is supplied by the fifth nerve. In order that distinct perception of smell should exist, it

is necessary that the nasal mucous membrane should be moist. The use of the sense of smell is, to guide the animal in the selection of food, and to the respiration of pure air. Foul smells are often, though not always, associated with unwholesome emanations.

CHAPTER XVI.

GENERATION AND DEVELOPMENT.

The fact that any animal or vegetable substance, when kept moist and exposed to the air and light, soon begins to teem with life, formerly led to the belief in the occurrence of spontaneous generation, and even animals so highly organised as flies or mice were supposed to originate without parentage. The application of more exact methods of observation to physiology has, however, shown that in proportion to the perfection of the means by which the decaying bodies of animals or plants are protected from the access of living animals or their ova or germs, the appearance of new life becomes more and more rare, until at length, when they are totally excluded, though chemical changes may take place which result in the decomposition of the body, no form of animal or plant life can be discerned. The difficulty of suggesting any mode of preventing the access of germs to an infusion of plant or animal tissue, satisfactory to an opponent, is, however, remarkably great, and attempts have even recently been made to demonstrate the appearance of life without the existence of parents, though the organisms thus believed to be produced belong to the simplest forms of life with which we are acquainted. If an infusion of hay,

turnip, carrot, muscle, nerve, or skin be enclosed in a tightly-stoppered vessel, and exposed to the warmth and light of the sun, it is found in a day or two to swarm with minute, and indeed microscopic, beings—monads, infusoria, microspores; but it is easy to suggest that the circumambient air contains enormous numbers of spores, which, though invisible even to microscopic investigation, may yet be capable of producing new life. The reply that has been made to this, and which appears at first sight satisfactory, is, that such infusions may be placed in vessels with long necks, and made to boil, which may reasonably be supposed to kill all germs, and that whilst boiling, the neck may be hermetically closed by fusion of the glass with a blow-pipe flame, and that still organisms appear in the infusion. It is here, however, that the controversy rests, and the misfortune is that the positive experiments of the one side are the negative of the other. Those who maintain the doctrine of *biogenesis*, and that life proceeds from life alone, contend that in proportion to the care with which the whole proceedings tending to exclude germs are conducted (as, for example, the purity of the surrounding air; the length of time the ebullition has been continued; the avoidance of the entrance of a bubble of air in the act of fusion of the neck, or, if this expedient be not adopted, the packing of the neck, made tortuous, and filled with wool to act as a filter) the more completely sterile do the infusions become; whilst those who hold the doctrine of *abiogenesis* can only point to the presence of life on the globe, and ask, apart from creation, how it could have originated, and why it should be held to be impossible that a certain aggregation of chemical elements should possess those properties to which the term "vital" is applied. Granting, then, that so far as we know at present, all life proceeds from some antecedent form of life, the

modes in which new creatures appear may be reduced to two, the *asexual* and the *sexual*. Both forms are met with in plants and both in animals.

The chief varieties of the *asexual* mode are fission, gemmation or proliferation, as in the evolution of young from detached buds, and parthenogenesis. The simplest form of asexual generation is that presented by the Amœba, in which the body separates into two parts, each of which is as capable as the other of maintaining its own life. This is termed *fission*. It is probably performed under the influence of abundant nourishment and a certain temperature. A form of fission is common in Algæ, in which the protoplasm of the parent cell breaks up into separate masses, which, growing, burst the cell, and begin life on their own account. In *gemmation*, an outgrowth takes place, without sexual connection, from some part of the parent, which under favourable circumstances may reproduce the entire plant or animal. In some instances the bud remains connected with the parent stem; in others it becomes detached. Gemmation may be coincident with the occurrence in the same organism of sexual generation. A third form is *conjugation*, or coalescence, seen in some of the lowest forms of life, as in the algæ and in the Gregarinida, when two neighbouring cells each develop a protrusion, and when these meet, the septa break down, the contents of the cells mingle, and a new individual appears between the parents. The process resembles in some important respects the sexual mode of reproduction. In *parthenogenesis* new individuals are developed from virgin females, by means of ova, without the intervention of a male. The remarkable mode of development termed the *alternation of generation* constitutes a kind of intermediate form between the sexual and asexual modes of reproduction, for whilst embryos are produced by sexual reproduction,

these develop into organisms which are capable of propagating their like in an asexual manner, sometimes for several generations, when they suddenly assume sexual characters, and once more produce their young by sexual generation. One of the examples which has been most carefully and completely followed is the tape-worm, which is an hermaphrodite animal, living a parasitic life within the intestinal canal, with testes and ovary in the same animal. Segments of the tape-worm containing numerous impregnated ova are discharged with the fæces, and are called *proglottides*. In the interior of each ovum an *embryo*, provided with six hooks, is developed, and enters the body of some other animal with its food; the act of digestion frees it from its covering, and it immediately bores its way into the tissues, and becomes a vesicular worm, or *cysticercus*. One or more heads or vesicles develop within the vesicle. The cysticercus is now swallowed by another animal, and the head fixes itself in the intestinal canal of the new host, and forms a *scolex*, which by budding produces a long chain of segments, each of which, when fully developed, is the sexually mature tænia.

Sexual generation is the mode in which reproduction is effected in all the higher forms of animals. It is usually and best accomplished in the maturity of life, after full growth and development are completed, and before the physical powers are weakened by the advance of age. It is the result of the union of a male element named the *sperm* with a female element named the *ovum*. In some instances, as in fishes, the fertilisation of the ova is effected without the body, but in the majority of cases the impregnation of the ovum takes place within the body. In some instances the ovum is sufficiently large to supply all the material for the growth and development of the young, and is, as in birds, discharged from the body, and kept warm

either by the heat of the body of the parents or by exposure to the sun's rays. In mammals, however, the ovum is very small, and is retained in the body of the uterus, from the vessels of which it indirectly receives its supplies of oxygen and of food.

Functions of the male organs.—The male organs are the penis and testes. The testes prepare the fertilising agent, or spermatic secretion. The penis serves as an intromittent organ, by which the sperm is injected into the neighbourhood of the os uteri, or directly into the cavity of that organ. For the structure of the testes and spermatozoa see Klein's "Elements of Histology," p. 249.

The **seminal fluid.**—The sperm or seminal fluid is semi-solid or gelatinous, of whitish colour, peculiar odour, which has been likened to that of moist dough, and which is developed only at the period of emission, as it is imperceptible in the fluid contained in the vesiculæ seminales, or in any of the other secretions which are discharged coincidently with the sperm, such as the prostatic secretion, or the secretion of Cowper's glands. Its reaction is slightly alkaline. Exposed to the air it dries up, and stiffens linen like starch. When such spots are moistened and examined with the microscope, spermatozoa may be recognised, the addition of carmine solution bringing the heads prominently into view. The spermatic fluid obtained from the vas deferens is pasty, whitish, and is composed of nine-tenths of spermatozoa and one-tenth clear fluid; but when it has reached the ampulla of the vas, it is mingled with a brownish fluid, which alters its colour and renders it thinner. In cases of repeated coitus at short intervals, the fluid contains few spermatozoa, and is chiefly composed of prostatic fluid and the mucus of the vesiculæ seminales. The object of the prostatic fluid seems to be to render it more fluid, and to facilitate the movement of the

spermatozoa. The chemical composition of the spermatic fluid is :

Water	88·0
Spermatin	6·0
Fat	2·5
Magnesium and calcium phosphate	3·0
Sodium phosphate	1·0
Ammoniaco-magnesian phosphate	a trace.

Spermatin is an organic substance, resembling mucin and albumin. It coagulates on the addition of alcohol, and the coagulum dissolves when treated with liquor potassæ; but when the potash is neutralised with nitric acid, it does not, like albumin, undergo precipitation. It also differs from albumin in not being coagulated by heat. Spermatin is chiefly formed in the vesiculæ seminales. The spermatozoa are formed in the tubuli seminiferi. They are not, as a rule, formed before the age of sixteen or seventeen. They continue to be produced to an advanced period of life, having been found at the age of ninety and upwards. They move in a spiral manner by a vibratile motion of the long tail. The movements are arrested by cold, the addition of a little snow stopping them in less than a minute, by the addition of acids, one part of hydrochloric acid in 7,500 of water rapidly killing them, and by various poisons, such as opium and strychnia. They are killed by a temperature of 50° C., and by the passage of an electric current. Their activity is favoured by the addition of slightly alkaline fluids, such as the serum of blood and milk; and they have been seen in action in the generative passages of the female eight or ten days after coition. It is owing to these movements that the spermatozoa are able to perforate the thick albuminous coating which surrounds the vitellus. The movements are not often perceptible in spermatozoa taken from the tubuli seminiferi, but are

apparent in those taken from the vas deferens or vesiculæ seminales. The motility of spermatozoa must not be confounded with their vitality. Their motility is the persistence of their movements; their vitality is the persistence of their power to fecundate the ova. In the practice of pisciculture the ova of the trout, salmon, or other fish, are obtained in a dry state by gentle pressure of the abdomen of the female over a vase. The spermatic fluid of the male is, by the same means, made to cover them. But the two may long remain in contact without fecundation occurring, the spermatozoa being motionless. As soon, however, as a little water is poured over them, the spermatozoa begin to move, and almost all the ova are fecundated in the trout in less than half a minute. The spermatozoa of man can traverse 2·7 mm. in the space of one minute. According to Fort, monorchids, or those in whom one testis has not descended, but remains in the abdomen, produce no spermatozoa on the side of the retained testis, but are capable of procreating children of both sexes with the other. Those in whom neither testis has descended are infertile, though the testes present their normal structure. The spermatic secretion is formed continuously, and though in great part re-absorbed, yet gradually accumulates in the vesiculæ seminales, from whence it is discharged, in the absence of all sexual excitement, in many cases perfectly naturally, about once in three weeks or a month. Self-abuse, too often practised by youths, is strongly to be deprecated, since it produces both mental and physical exhaustion, incapacity for work, and unwholesome trains of thought.

Erection.—Under ordinary circumstances the penis is soft, flexible, pendulous, and of small volume. During sexual excitement it acquires a larger volume,

and becomes erect, rigid, hotter, and much more sensitive. The object of these changes is to render it efficient as an intromittent organ, and to enable it to conduct and deposit the semen at or near the mouth of the uterus. The cause of erection has been the subject of much controversy. There can be no doubt that the vessels not only contain more blood, but that the circulation through them is more active. The pressure of the blood in the vessels rises to one-sixth that of the pressure in the carotid. The arteries undergo active dilatation under the influence of the vaso-dilator fibres contained in the nervi erigentes, which in the dog arise chiefly from the second sacral nerve, and contain ganglion cells in their course. The *centre* for these nerves is in the lower part of the spinal cord, and it may be excited in various ways, as by stimulation of the *sensory* nerves of the penis, and by psychical processes. The fulness of the vessels thus induced is aided by the contractions of the erectores penis, which, forming a tendinous expansion over the dorsal vein of the penis, hinder the return of blood; and also by the contractions of the transversus perinæi profundus, and of the accelerator urinæ, which contribute to render the bulbus urethræ rigid.

Ejaculation.—The semen is stored up in the vesiculæ seminales, which are long sacculated tubes with muscular walls, contractions of which are induced in response to stimulation of the nerves of the penis. The fluid they discharge is driven along the urethra by the contraction of the muscular walls of that tube, of the accelerator urinæ and erector penis muscle. The nervous circle is completed through the *sensory* nerves of the penis; the ejaculator, or genito-spinal *centre* in the lower part of the spinal cord, and the *motor* fibres which are distributed to the vesiculæ and to the erector muscles. The sphincter vesicæ is spasmodically contracted, to prevent the entrance of

the fluid into the bladder; and this is further prevented by the swelling of the verumontanum. The quantity discharged at each emission varies from one to two or three drachms.

Menstruation.—This periodical occurrence is coincident with the rupture of a Graafian follicle, and the setting free of an ovum. It is characterised by the discharge through the vagina from the uterus of a variable quantity of blood, which lasts for one, two, or three days, once in four weeks. It is the result of a process termed *ovulation*, which produces a flush of blood to the whole of the generative apparatus; but it is long preceded by a growth of the tunica propria of the Graafian follicle which is accompanied with abundant formation of vascular loops, that fill its cavity and constitute the expelling force, resulting in the extrusion of an ovum; whilst the expulsion is facilitated by fatty metamorphosis of the follicular wall, which renders it more friable (Fig. 29). The distension of the follicle probably constitutes a stimulus to the nerves supplying the ovary, and the afflux of blood to the generative organs is a reflex action. The congestion thus induced causes increased transudation into the follicle, diapedesis of numerous white corpuscles, and increased thickening of the wall, which at length gives way at its crown or weakest part, which is destitute of blood-vessels and lymphatics, and the ovum escapes. The whole of the generative organs participate in the congestion, the mucous membrane of the uterus becoming thicker, more spongy, and hyperæmic; forming the *decidua menstrualis*, which differs from the decidua of the impregnated uterus in the small size of the spheroidal cells that are developed in the interglandular tissue. According to Dr. Williams, the epithelium and the uterine glands, with the mucous membrane, undergo fatty degeneration, and are in great part thrown off, renewal taking place from the

deeper portions which still remain. With the changes in the generative organs other reflex or consensual effects are observed. The breasts enlarge and are rendered more sensitive. There is some gastric disturbance, with general lassitude and indisposition to



Fig. 29.—Mature Graafian Follicle containing an Ovum, which is about to escape through a rupture of the wall of the Follicle, carrying with it some of the cells of the surrounding Discus Proligerus.

work. The quantity of blood discharged varies considerably, but is estimated as amounting on the average to about 300 grammes. It presents no peculiarities, except that on account of its admixture with mucus and other materials secreted by the vaginal mucous membrane, it has little or no tendency to coagulate. The majority of women menstruate during the first quarter of the moon, few only at the

time of the new or full moon. The first occurrence of menstruation is usually between the thirteenth and the fifteenth year. Brunettes are said to commence earlier than blondes, but in this respect heredity, social position, and mode of life, together with climatic conditions, are powerful factors. Warmth, abundant food, and luxurious habits of life tend to render its appearance earlier. Menstruation is a sign of sexual maturity, and as long as it lasts it is possible that a woman may bear a child. It usually ceases, after first becoming irregular, between the ages of forty-five and fifty.

Formation of corpus luteum.—As soon as the ovum has escaped, the cavity of the Graafian follicle in which it was contained becomes filled with blood, which soon coagulates, whilst the cells of the membrana granulosa disintegrate. The rupture of the ovarian wall cicatrises, the serum of the coagulated blood is re-absorbed, the hæmoglobin becomes converted into hæmatoidin, and the vascular wall of the follicle develops villous-like processes, which project into its interior, and contain many capillaries and numerous cells. Diapedesis of white corpuscles takes place to a large extent. The cells of the membrana granulosa multiply and form laminæ, which are superimposed upon each other, and subsequently undergo fatty degeneration with the formation of lutein and fat, the yellow colour of which has led to the application of the term *corpus luteum spurium* to the now gradually disappearing remains of the Graafian follicle, which is scarcely visible at the expiration of four weeks. If pregnancy take place, the larger supply of blood to the whole of the generative apparatus causes the corpus luteum, then called the *corpus luteum verum*, to increase to so great an extent, that at the time of delivery it may measure nearly half an inch in length, whilst its colour is much deeper. and some traces of it remain

for years. Menstruation is, as a rule, arrested by the occurrence of pregnancy.

Maturation of the ovum.—Before impregnation, an ovum undergoes a series of changes to prepare it for the action of the spermatozoa. These changes are akin to those which have been observed in a cell previous to its division, and which have been described by Klein in his "Elements of Histology" (p. 7). Fol, who investigated the eggs of the starfish, noticed that the first change in the ripe ovum consisted in the germinal vesicle becoming indistinct, owing to its

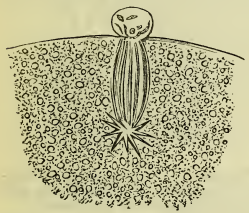


Fig. 29A. — Maturing Ovum, showing Formation of Polar Cell, Spindle, and Female Pronucleus.

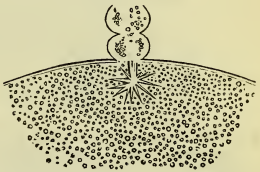


Fig. 29B.—Detachment of a Second Polar Cell.

substance fusing with the vitellus. Subsequent changes in the germinal vesicle, and in the adjoining protoplasm, led to the formation of two asters, connected by means of a spindle, the axis of which was parallel to the surface of the egg. At a later period the spindle becomes vertical, and one axis protrudes through the vitellin membrane to form the polar cell or directive corpuscle. The polar cell is subsequently constricted off, and by similar changes occurring in the spindle a second body is formed and got rid of. The other aster, with such portions of the spindle as remain after this formation of polar cells, forms a new nucleus for the ovum, and is named the *female pronucleus*.

Fecundation.—This consists in the fusion of the male with the female element, the spermatozoon with the ovum. In order that it should be effected it is necessary that the spermatozoa, after entrance into the uterus, should be living and active, and that in the female the passage from the ovary to the



Fig. 29c.—Spermatozoa about to penetrate the Ovum, which presents a Colliculus to meet them.



Fig. 29d.—Penetration of a Spermatozoon into an Ovum, and formation of a Membrane.

vagina should be free. The female pronucleus, which, after the formation of the second polar body, was situated near the periphery of the ovum, travels again towards the centre, its position being marked by the radial striation of the protoplasm around it. If a spermatozoon now gains access to the ovum thus prepared to receive it, the surface becomes raised into a small prominence. The head of the spermatozoon passes through this prominence into the egg, the tail undergoing certain changes, but finally fusing with the protoplasm of the ovum. As soon as the head of the spermatozoon has passed into the ovum, the superficial portion of protoplasm separates to form a distinct membrane round the egg, which prevents the entrance of other spermatozoa. The head of the spermatozoon

which has thus gained access to the egg is termed the *male pronucleus.* It increases in size, whilst the

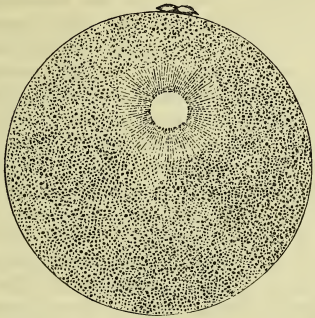


Fig. 29F.—Ovum with two Polar Cells and Female Pronucleus, surrounded by Radial Striæ.

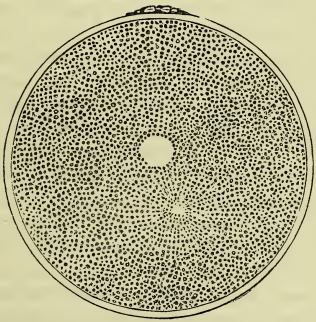


Fig. 29F.—Ovum with Male and Female Pronucleus, and with radial striation of the Protoplasm around the former.

protoplasm around it becomes radiately striated ; ultimately it fuses with the female pronucleus to form the fertilised nucleus, or first segmentation nucleus.

Mr. Balfour, from whose work on "Comparative Embryology" the above account of the maturation and fecundation of the ovum has been taken, draws attention to the fact that the female pronucleus is the product of the nucleus of the primitive ovum, whilst the male pronucleus is the metamorphosed head of the spermatozoon, containing part of the nucleus of the primitive spermatic cell, since the whole of the spermatozoa derived from a spermospore (the cell which gives rise by division to the spermatozoa) are together equivalent to one ovum. The spermatic cells originate from the cells which are at first indistinguishable from the primitive ova, so that the fusion which takes place between the male and female elements is the fusion of morphologically similar parts. It appears probable that a single spermatozoon is alone required for the perfect fecundation of an ovum; but there is at present insufficient evidence upon this point to draw any reliable conclusion.

In some animals, as in most of the carnivora and in ruminants, there is a definite time, known as the rut, or rutting season, at which alone the female will permit coitus to take place, and when fecundation occurs; but in other instances, as amongst rodents, marsupials, and others, coitus is frequent, and there is no definite season for the fertilisation of the ova. In man, coition and fecundation may apparently occur at any period. Fertilisation of an ovum is not necessarily coincident with coitus; nor can the females, except in rare cases, state precisely when it occurs. In all instances the spermatozoa must make their way, by virtue of their vibratile movements, along the cervix uteri into the body of that organ, and the occurrence of ovarian, or of extra uterine, or of tubal pregnancy, in which the fecundated ovum begins to develop within the ovary, or becomes attached to some part of the

peritoneal cavity, having missed the upper opening of the Fallopian tube, or develops in the Fallopian tube itself, conclusively proves that the spermatozoa can make their way through the whole length of the uterus and Fallopian tube to the ovary. It is probable, however, that impregnation generally takes place in the upper part of the Fallopian tube, whilst the ovum is descending partly by the action of the vibratile cilia that line the tube, and partly by the peristaltic action of the muscular walls; and up to which point the spermatozoa have made their way by their own movement in opposition to that of the uterine cilia. The unfecundated ovum descends through the uterus, and is dissolved or discharged; the fertilised ovum, on the contrary, is arrested in its course through the uterus, probably owing to the greater turgidity of its walls when fecundation has taken place, and becoming attached undergoes its full development. According to Landois, twins, or double impregnation, occurs once in 87 deliveries, though more frequently in hot climates; three at a birth once in 7,600; four at a birth once in 330,000. More than six at a birth have not been observed. The average number of impregnations for each woman is $4\frac{1}{2}$.

The **ovum.**—The ovum, or egg, is produced by the female. It is small in man, but very large in the bird or reptile, and its several parts are best studied in these animals. In its young condition in all animals it is a simple cell.

Ovum of the bird.—The parts of the ovum of a bird are: 1. An external calcareous coating or *shell* which is porous, and permits the passage of air and moisture. 2. *Two thin membranes*, which, closely applied to each other throughout the greater part of their extent, become separated, shortly after the egg has been laid, at the large end of the egg, and

contain a bubble of air between them at this point. 3. Next comes the *albumen*, which is deposited in layers, and can be detached in a hard-boiled egg in flakes which have a spiral direction; the outer layer of the albumen is less firm and consistent than the inner. 4. At each end of the egg the albumen forms a distinct gelatinous mass, which stretches between the yolk and the shell, and which resists coagulation by heat rather longer than the other parts of the albumen. These masses are twisted spirally, but in opposite directions, and are believed to aid in keeping the yolk in position. They are named the *chalazæ*. 5. If the albumen be entirely removed the yolk is seen to be surrounded by a delicate membrane, termed the *vitelline membrane*. 6. If an egg be laid on its side and the shell be broken by gentle taps, it is easy to pick away the shell and lining membrane over a space about equal to a threepenny piece without damaging the yolk. The part of the yolk exposed presents a small round spot of lighter colour than the rest of the yolk, which is an indication of a separation of the yolk into two parts, which have a marked difference in their use and purpose; the light yolk is the *germ yolk*, or *blastoderm*, which alone undergoes segmentation, and is directly converted into the body of the embryo; the yellow yolk, though it ministers to the development and growth of the embryo, does not undergo segmentation, and is hence called the "food yolk."

The circular patch of white yolk, also named the *cicatricula* or *tread*, may be seen on section to give off a process that dips into the yellow yolk to near its middle, where it dilates into a kind of vesicle; the whole somewhat resembling a Florence oil flask, the mouth of which is a little expanded. Whatever part of the side of the shell is chipped away, the blastoderm invariably comes into view, and the yolk being lighter

than the albumin floats up to near the surface. 6. The yellow yolk when boiled, or otherwise hardened, presents concentric markings, that are termed *halones*, and it is then seen to be invested externally by a thin layer of the white yolk prolonged from the margin of the blastoderm. The yellow yolk is composed of small spheroids, which contain no nucleus, but are filled with minute highly refractile albuminous granules. The white yolk is also composed of spheroids, but these differ from the spheroids of the yellow yolk in being smaller and in containing a nucleus. Eggs which, like those of the fowl, consist of two parts, one of which undergoes segmentation, whilst the other does not, are called "meroblastic." Eggs which, like those of mammalia, undergo total segmentation, are termed "holoblastic."

Chemical composition of the fowl's egg.—The shell is composed of 4·15 per cent. of organic substance, chiefly albumen, impregnated with calcium carbonate to the extent of 93·7 per cent., and containing also small quantities of magnesium carbonate (1·39 per cent), calcium phosphate (0·76), and iron phosphate. The yolk consists of 47·1 per cent. of water, 15·6 per cent. of albumin, 31·3 per cent. of ether extract, chiefly fats, 4·8 per cent. of alcohol, and 0·96 per cent. of inorganic salts. Amongst the substances which have been isolated are : vitellin, which is the characteristic albuminous compound of the yolk ; nuclein, chiefly obtained from the white yolk ; lecithin, glycerin, phosphoric acid, cholesterin, palmitin and olein, a pigment named lutein, glycogen, and grape sugar.

Ovum of man.—The human ovum differs in several particulars from that of the bird. It is extremely small, having a diameter of only about $\frac{1}{120}$th of an inch. It has an external investment named the *zona pellucida* (Fig. 30, *b*), which is of considerable thickness, and capable of resisting tolerably strong

pressure, returning to its spheroidal form as soon as the pressure is removed, by virtue of its elasticity. It presents a fine radial striation, due to the presence of fine canals. This membrane (*zona radiata*) corresponds apparently to the vitelline membrane of the

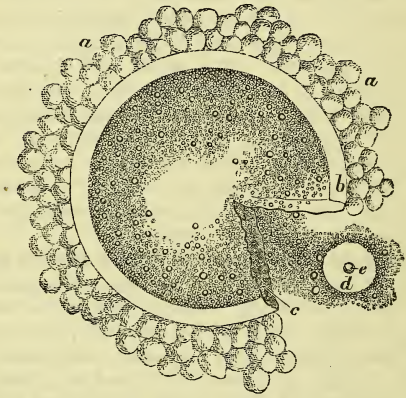


Fig. 30.—Ovum of Mammal.

a, Cells of discus proligerus; *b*, zona pellucida; *c*, vitellus; *d*, germinal vesicle; *e*, germinal spot.

egg of the bird, for it directly invests the vitellus, which is here granular and contractile. In the midst of the vitellus is a nucleus named the *germinal vesicle.* or vesicle of Purkinje, containing nucleo-plasma and a nucleolus named the *germinal spot,* or spot of Wagner, both of which may be seen under the microscope. Besides the nucleolus, some small corpuscles have been noticed by v. Beneden, which have been named *pseudo-nuclear* bodies.

Mode of origin of the ovum. — If a transverse section be made through the body of the embryo

of a fowl about the close of the fourth day, the abdominal cavity is seen to be lined by pavement epithelium, which becomes columnar at the level of the Wolffian body (*see* Fig. 31), and is here named the *germinal epithelium.* As the embryo develops, this columnar epithelium becomes limited to the inner and outer parts of the surface of the Wolffian body; the intermediate cells being flat. The *canal* or *duct of Müller*, which subsequently becomes the oviduct, is formed at the expense of the *external* germinal epithelium; the ovary, or sexual gland of the female, is developed

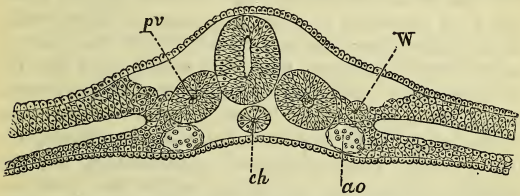


Fig .31.—Diagram showing early Differentiation of Parts in Blastoderm. *ch*, Chorda dorsalis; *pv*, provertebræ; *W*, Wolffian body; *ao*, aorta.

from the *internal* germinal epithelium, for in the midst of these columnar cells other cells make their appearance, which are larger, isolated, and spheroidal; these are the *primordial ovules.* These ovules, or female germs, exist at an early period in both sexes. In the male, according to Waldeyer, they disappear, the male elements developing from the Wolffian canal; but according to Semper, both male and female elements originate from the columnar epithelium.

Development of the ovum.—The ovum, as it descends the Fallopian tube, usually has numerous cells of the discus proligerus still adherent to it. In some animals, as the rabbit, the ovum receives an albuminous covering of considerable thickness, whilst in the dog it is very thin. *Segmentation* commences

during its descent. The manner of segmentation varies in different groups of animals. Eggs which are hatched within the body of the parent are provided with a small amount of yolk. In such cases the eggs may segment unequally, as in the frog, in which the upper portion of the egg divides to form a number of small cells, forming the roof of the segmentation cavity, whilst the lower portion consists of larger yolk containing cells. In other forms the egg divides into a number of equal segments. In both these cases the eggs divide up entirely, and they are therefore known as *holoblastic* ova. In the eggs of birds, the food material, or yolk, is present in larger quantities, since they are incubated outside the parent, and therefore require that the entire food for the development of the various tissues should be present when the egg is laid. These eggs are called *meroblastic*, since only a portion of their substance, viz. the germinal disc, undergoes segmentation, the rest usually forming an appendage called the yolk sac. During the process of unequal holoblastic segmentation, such as is supposed to occur in the human ovum, a groove forms, which speedily divides the ovum into two parts, of which one, named the *epiblastic sphere*, is larger and more transparent than the smaller, or *hypoblastic*, sphere. Each sphere soon undergoes subdivision into 2, 4, 8, 16 spheres, and so on, but with such change of position that at the close of segmentation (that is, at the close of the third day in the rabbit, and about the eighth in the human embryo) the larger granular hypoblastic spheres constitute a central solid mass, almost entirely surrounded by the smaller, clearer, and somewhat cubical epiblastic spheres. The segmented ovum now enters the uterus, and undergoes a series of changes, which result in the formation of the *blastodermic vesicle*. This is produced by the separation of the epiblast from the hypoblast,

and by the formation of a cavity in the centre of the ovum filled with fluid. The greater part of the walls of this cavity are formed at first of a single row of flattened epiblastic cells, whilst the hypoblast cells form a small lens-shaped mass attached to the inner side of the epiblast cells; but very soon the hypoblast cells spread out on the inner side of the epiblast, the central thickening, however, forming an opaque circular spot on the blastoderm, which is the commencement of the *embryonic area*. A day or two later this spot presents three layers, a new intermediate layer, termed the *mesoblast*, having made its appearance.

The mesoblast is derived in part as a proliferation of cells from the epiblast, and in part from cells which separate as plates from the hypoblast. The cells from these two sources soon become blended, and at an early period in the life of the embryo are indistinguishable from each other (Balfour).

The blastodermic vesicle now comes to present three areas: (1) The embryonic area, formed of three layers, epiblast, mesoblast, and hypoblast; (2) the ring around the embryonic area, where the walls of the vesicle are formed of epiblast and hypoblast; (3) the area beyond this again, where the vesicle is formed of epiblast only. Speaking generally, the *epiblast* gives rise to the central nervous system, to the epidermis and epidermoid tissues, as the hair and nails, and to the epithelium of the organs of sense; the *mesoblast* forms the greater part of the tissues of the body, such as the cutis, muscles, bones, and the large glands; whilst from the *hypoblast* originate the epithelium of the intestines and the cells lining the ducts of those glands which arise from it by a process of involution. The blood and blood-vessels and connective tissue arise in the fowl from the elements of the white yolk which lie external to the embryonal rudiment,

and have hence been called *parablastic* formations in opposition to the *archiblastic* formations which arise from one or other of the three layers of the embryo.

Primitive streak.—Medullary folds.—Early on the seventh day in the rabbit the embryonic area, previously oval, becomes pyriform, and at its posterior and narrower end a *primitive streak* makes its appearance, due to a proliferation of rounded cells from the epiblast. This is a transient feature in the process of development, and it rapidly disappears. The significance of the primitive groove is not yet fully understood. The embryo is developed in the more anterior portion of the area pellucida, and is only indirectly continuous with the primitive groove which lies in the axis of the primitive streak. On the eighth day two folds arise, bounding a shallow median groove. These meet in front, and diverge behind, enclosing between them the front end of the primitive streak. They are the *medullary folds*, and constitute the first definite traces of the embryo. The thickened axial portion of hypoblast beneath and between the medullary folds becomes separated from the lateral parts and forms the *notochord*, the fore part first becoming distinct. That part of the blastodermic vesicle which is included in the embryonic area alone takes part in the formation of the embryo; the remaining, or non-embryonic part, forms the *umbilical vesicle*, which is particularly well seen in fish, where it is large, and long remains visible as a sac appended to the body. The umbilical vesicle contains the food yolk,

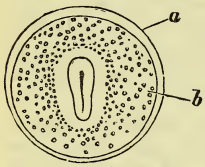


Fig. 32.—Ovum of Fowl, with Primitive Streak, surrounded by the Area Pellucida, which is bounded by a Line, and is Pyriform, and by the Area Opaca, which is Oval.

a, Zona pellucida; *b*, vitellus.

which is very small in quantity in mammals, and is gradually absorbed, being applied to the nutrition of the growing embryo. The lateral masses of mesoblast, from which the notochord has separated, begin to divide into a vertebral zone adjoining the embryo and a more peripheral lateral zone. The vertebral zone exhibits indications of two somites, the foremost of which marks the junction of the cephalic region and trunk. A delicate clear ring now appears around the embryonic area, which is believed to represent the peripheral part of the *area pellucida* of birds, and external to this is a well-defined *area vasculosa*. Even at this early period, before any folding off of the embryo has occurred, traces of the heart are visible, in the form of two tube-like structures running longitudinally in the lateral masses of the mesoblast. In the process of the folding off of the embryo the head fold appears first, and is deepest, and it is soon followed by the tail fold. The medullary groove, still open, now begins to close, from before backwards. Nearly coincidently with the formation of the primary vertebræ, a fissure appears in the lateral masses of the mesoblast, which is the commencement of the *pleuro-*

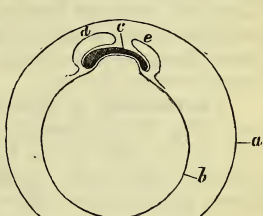


Fig. 33. — Diagram showing the gradual folding off of the Embryo, which comes to be seated on an eminence, and has a curved form.

a, Zona pellucida; *b*, vitellus; *c*, embryo; *d*, *e*, folds of amnion.

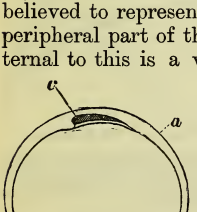


Fig. 34. — Formation of Head fold.

a, Zona pellucida; *b*, vitellus; *c*, head fold.

peritoneal cavity; the lower lamina is the *splanchnopleure*, which, folding inwards sharply, forms the walls of the intestine, which is lined by the hypoblast; whilst the outer, or upper, lamina is named the *somatopleure*, and also folding inwards, but with a much wider curve, forms the wall of the body. The heart appears in the space between the two.

Formation of the amnion.—When the embryo (Fig. 35) has become separated off by an inflection of the wall of the blastodermic vesicle from the general yolk cavity, a circular fold of the somatopleure and epiblast arises (*ks, ss*), the circumference

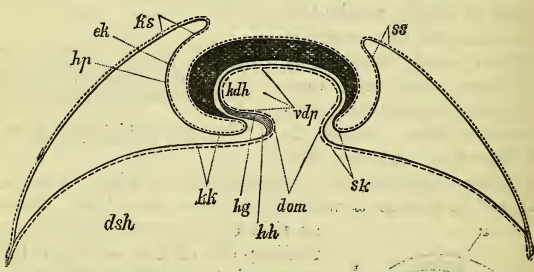


Fig. 35.—Diagram to show the mode of Origin of the Amnion.

hp, Somatopleure; *ks*, head fold of amnion; *ss*, tail fold of amnion; *ek*, epiblast; *kk*, head cap; *sk*, tail cap; *dsh*, cavity of the yolk sac; *dom*, ductus omphalo mesentericus or omphalo-mesaraicus; *kdh*, pharyngeal, or anterior portion of intestinal cavity; *vdp*, hypoblast lining the cavity of the intestine; *hg*, rudiment of heart; *hh*, part of pleuro-peritoneal cavity.

of which, gradually approximating towards the middle of the back of the embryo, ultimately meets, and the double septum existing at all points is absorbed. The embryo thus comes to be invested, except below, by a membranous sac, which is continuous with the skin, and which is formed of the somatopleure, lined by the epiblast. Fluid is secreted both within and without the sac. The fluid between the skin of the embryo and the inner layer of the sac occupies the

cavity of the amnion, and is termed the *liquor amnii*, whilst the free membrane separating the two portions of fluid is the true amnion. The outer layer of the sac, consisting of somatopleure internally and epiblast externally, which is called the *false amnion*, or *subzonal membrane*, soon coalesces with the vitelline membrane,

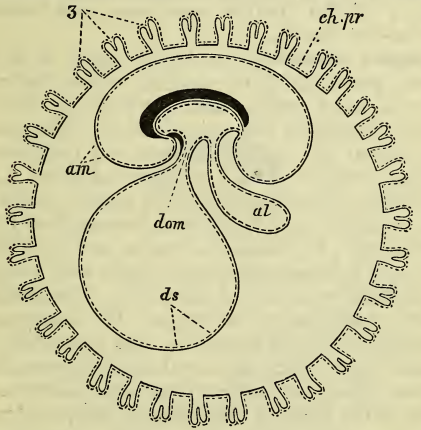


Fig. 36.—Diagram to show the complete Formation of the Amnion.
am, Amnion; *al*, allantois; *dom*, umbilical duct; *ds*, umbilical vesicle; 3, villi; *ch. pr.*, chorium primitivum.

and the fluid between it and the true amnion undergoes absorption. The amnion may now be regarded as a serous membrane, being a continuous sheet of membrane, and having an internal or visceral, and an external or parietal layer. The visceral layer, near the point where it becomes continuous with the skin of the embryo, curves downwards and inwards (*sk*, Fig. 35), and comes to invest the vitelline duct (*dom*), and thus ultimately forms a tubular sheath around the umbilical cord. The amnion possesses some contractile power,

owing to the presence of fusiform cells of unstriated muscular tissue, which are derived from the somatopleure. It executes slow rhythmical pulsations, which rock the embryo to and fro in the egg. The serous layer (*ch.pr*, Fig. 36) sends forth numerous processes, or villi, which project from the whole periphery of the vitelline membrane, and constitute the *primitive chorion*.

Liquor amnii.—The liquor amnii is a clear yellowish-green fluid, of peculiar odour, in which epidermis, hairs, scales, and particles of fat, cast off from the skin of the embryo, float. The quantity is larger near the middle of pregnancy than towards the close, when it usually amounts to about a pint. Its reaction is alkaline; its specific gravity varies from 1·002 to 1·028, and in general it resembles diluted blood serum. It contains albumin and globulin-like substances, a fermentable sugar, lactic acid, kreatinin, urea, and the usual salts of the blood. The urea is excreted by the kidneys of the fœtus. The liquor amnii is essentially formed by the fœtus, part proceeding from the skin, part from the fœtal chorionic capillaries, which are closely applied to the amnion and to the vasa propria of the limiting membrane of the placenta, and partly from the kidneys, the evidence of which is the very small quantity of liquor amnii found in cases where the fœtal kidneys are congenitally absent. A portion, however, is probably also supplied by the mother from the numerous vessels of the decidua vera. The uses of the liquor amnii are to fill the uterine cavity evenly; to protect the fœtus from injury through the abdominal walls of the mother; to give room for, and to prevent the mother from being incommoded by, the fœtus; and to facilitate delivery by forming an elastic pad, equably dilating the external parts.

The **allantois.**—This organ is far more highly developed in reptiles and birds than in mammals. It

is the means by which the blood is aërated, a process which in mammals is very early effected by the interchange of gases between a thin layer of the fœtal blood and a corresponding layer of the maternal blood in the placenta, but which is provided for in birds and reptiles by the expansion of the vascular

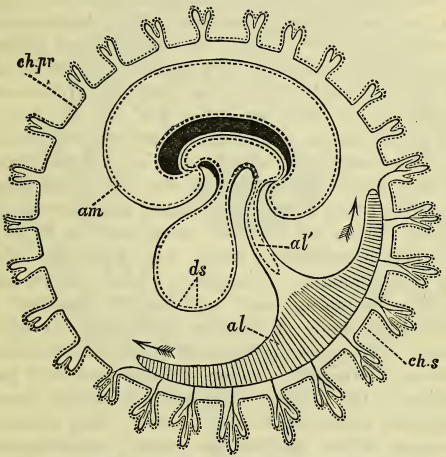


Fig. 37.—Diagram to show the Formation of the Allantois.
ch.pr, Primary chorion ; *ch.s*, secondary chorion ; *am*, amnion ; *ds*, remains of yolk sac; *al*, allantois ; *al'*, neck of allantois.

allantois immediately beneath the shell of the egg. It arises as two projections, which soon coalesce, from the splanchno-pleure at the posterior extremity of the embryo. It is seen in Fig. 37, where it is marked *al*, *al'*, and grows first into the pleuro-peritoneal cavity of the embryo and then into the space between the true and the false amniotic cavities. It gradually extends over the embryo in the direction of the arrows in Fig.

37, and lies over the embryo and true amnion immediately beneath the shell in the fowl's egg, from which it is separated only by the false amnion and vitelline membrane. It never attains this size in mammals. From its mode of origin it is necessarily at first composed of two layers, the endoderm and that portion of the mesoblast which forms the fibro-muscular layer of the intestine ; but as it increases, the endodermal layer *al'* ceases to grow, whilst the mesodermal plate enlarging applies itself to the primitive chorion (*ch.pr*, Fig. 37). The allantois is the medium of the second circulation of the embryo, for in it run the embryonic vessels, the umbilical artery, and umbilical vein, the branches of which reaching the periphery in this way, shoot into certain of the villi of the chorion, converting this from the primary into the secondary chorion. Some of the villi, as shown at *ch.pr* (Fig. 37), remain relatively small, and form the *chorion lævе*, and ultimately disappear ; whilst others, enlarging *ch.s*, becoming leafy and highly vascular, have received the name of *chorion frondosum*, or *placenta fœtalis*. The commencement or root of the allantois remains as the urinary bladder, its outer part, still patent, forming in the mammal the urachus, which, however, disappears about the second month. The allantois is the organ which receives the urinary constituents, for the excretory ducts of the primary kidneys, or Wolffian ducts, open into it, and the secretion, passing by the allantois through the umbilicus, enters the peripheral part of the urinary sac. The fluid of the allantois has been found to contain urate of ammonia and soda, urea, allantoin, grape sugar, and salts.

The **placenta fœtalis,** the origin of which from the amnion and allantois has just been described, applies itself to a corresponding hypertrophied portion of the mucous membrane of the uterus, named the *placenta uterina* (Fig. 38, *pl.u*). Whilst the yolk

sac (*ds*) gradually diminishes in size, owing to the absorption of its contents, the amnion enlarges, and everywhere becomes applied to the inner surface

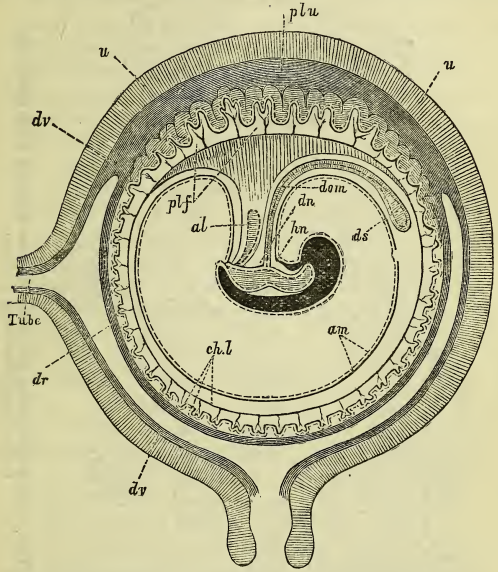


Fig. 33.—Diagram to show the Formation of the Placenta.

u, Uterus; *dv*, decidua vera; *dr*, decidua reflexa; *ch.l*, chorion; *am*, amnion; *al*, allantois; *ds*, vitelline duct and sac; *plf*, placenta fœtalis; *pl.u*, placenta uterina; *dom*, ductus omphalo-mesentericus; *hn*, the point of junction of the amnion with the skin; *dn*, the cavity of the amnion.

of the chorion verum, formed by the union of the chorion primitivum and allantois. It is seen to invest the vitelline duct (*dom*), the stalk of the allantois, and the vessels it supports, which collectively form the umbilical cord connecting the embryo and the uterus. The embryo is thus contained within two concentrically arranged vesicles, the chorion and the

amnion, which are both continuous with the body of the embryo at the umbilicus or navel. But it receives

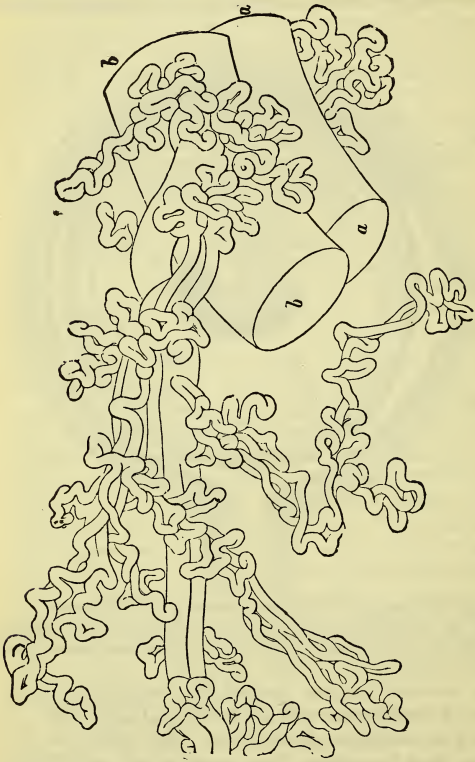


Fig. 39. The Villi of the Fœtal portion of a mature Human Placenta × 100 diam.; the capillaries are filled with injection.
a, Artery; *b*, vein.

additional coverings from the mother, for as soon as the fecundated ovum is arrested in its passage down

the uterus, the uterine mucous membrane begins to grow up around it like the cup of an acorn, and ultimately entirely invests it. The proper wall of the uterus in the rest of its extent also increases in thickness and vascularity, and, as the fœtus enlarges, that portion which has grown over it, and which is known as the *decidua reflexa*, comes into contact with the true mucous membrane, which is termed the *decidua vera*. A space exists between the decidua vera and reflexa up to about the third month, but at the fourth month the whole cavity of the uterus is filled with the ovum and the decidua reflexa. At one limited spot (*uu*, Fig. 38) the ovum lies in direct contact with the decidua vera, but in the rest of its extent it is separated from the decidua vera by the decidua reflexa. This spot is the *decidua serotina;* it becomes the placenta. At this spot the uterine vessels undergo great enlargement, and form irregular cavernous spaces, into which the villi of the chorion dip. The vascular villi of the fœtus are received into the wide blood-vessels of the uterine placenta, so that the capillaries of the fœtal system are bathed in uterine sinuses; and although there is no direct communication between the blood of the mother and of the fœtus, a free interchange of gases takes place; and whilst the uterine blood supplies nutritious matter to the fœtus, the fœtal blood yields up to it again effete and disintegrated material. The ends of the villi are formed by the inosculating

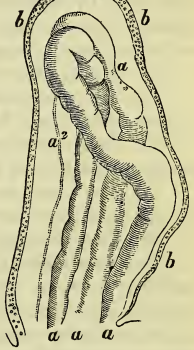


Fig. 40.—The Extremity of a Villus taken from a fresh Placenta.

a a, *b*, Loops filled with blood; a^2, empty loop; *b*, margin of pellucid villus.

loops of the small arteries and veins of the fœtus, which are characterised by the peculiarity of making several turns into different loops before terminating in a vein.

The structure of the placenta is somewhat complicated. The maternal portion forms the general framework, into depressions of which are received the convoluted vessels distributed to the chorionic villi of the fœtus. The maternal placenta presents a cavernous texture, and sections exhibit wide spaces and cavities, which intercommunicate freely, and are separated by trabeculæ. If a vertical section be made through the placenta, the following structures are met with in passing from the uterus to the umbilical cord:

(1) The decidua serotina.

(2) The intermediate cavernous portion, filled with hypertrophied and frondose fœtal villi.

(3) The subchorionic septum, which bounds the maternal portion of the placenta.

(4) The placental part of the chorion.

(5) The gelatinous layer.

(6) The placental part of the amnion.

The **umbilical cord.**—This constitutes the connection between the mother and the fœtus. Its average length is 50 to 55 ctm., or about 20 inches. It contains the two umbilical arteries, the umbilical vein, the remains of the allantois with the urachus, and is invested by the amnion. It presents a spiral twisting, which is usually, though not always, from right to left in passing from the fœtus towards the placenta.

Development of the heart and vessels.—The heart is formed in the head fold of the embryo, in the general pleuro-peritoneal cavity formed by the separation of the splanchno-pleure from the somato-pleure. In the duck it has assumed a flask-like form as early as the first half of the second day. At its anterior end is a slight swelling indicating the future

folds of the splanchnopleure. In front it divides into two primitive aortæ, both of which curve upwards and then backwards, pursuing a parallel course towards the tail in the mesoblast on each side of the notochord, immediately beneath the protovertebræ. About the middle of their course each gives off, at right angles to the axis of the embryo, the omphalo-mesaraic artery, which is distributed over the pellucid and vascular areas. The vascular area is bounded by the *sinus* or *vena terminalis*. The blood returns from the vascular and pellucid areas and by the omphalo-mesaraic veins enters the heart behind. *This is the first circulation of the embryo.* Both vessels and corpuscles are formed entirely from the cells of the mesoblast, some coalescing to form the walls of the vessels, others remaining free and becoming converted into blood corpuscles. The rhythmic movements of the heart are visible in the course of the second day of incubation in the fowl, before any differentiation of tissue can be observed.

The aortic arches.—The two primitive aortæ, springing from the bulbus arteriosus, unite above the alimentary canal, at the back of the embryo, to form the 1st pair of aortic arches. At a later period a 2nd, 3rd, 4th, and 5th pair of arches are formed behind the first pair, though only three pairs are patent at any one time. Of these five pairs, the central portions of the two arches situated most anteriorly disappear at an early period. The first pair, before it disappears, sends off a branch on each side towards the head. Of these, one is the direct continuation of the bulbus arteriosus, and is ultimately called the external carotid; whilst the other, starting from the point where the aortic arch joins its fellow to form the dorsal aorta, is the internal carotid. By the disappearance of the 1st and 2nd pairs of arches, the carotids eventually arise from the two sides of the 3rd arch. At first the aorta and pulmonary

arteries form a single vessel arising from the heart. As development proceeds, however, the common trunk, or bulbus arteriosus, divides into an aorta, which retains its connection with the 3rd and 4th arches, whilst the left 5th arch is continuous with the other division, called subsequently the pulmonary artery, the right 5th arch disappearing or remaining only in rudiment, as the ductus Botalli, or ductus arteriosus; whilst the branch of communication between the 3rd and 4th arches becomes smaller. The 4th arch of the left side increases in size, and represents the permanent aorta, its fellow of the opposite side remaining as the right subclavian.

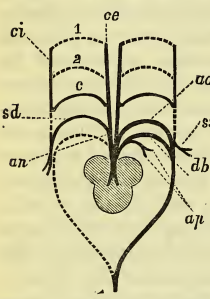


Fig. 7.—Diagram of the development of the Aortic Arches in a Mammal.

1, First aortic arch, which ultimately disappears; 2, second aortic arch, which undergoes the same fate; *c*, third aortic arch; *ci*, internal carotid; *ce*, external carotid, an innominate artery; *sd*, fourth arch of the right side dividing into the right vertebral and subclavian arteries; the dotted line below it represents the transient fifth arch; *aa*, the left fourth arch, communicating by *db*, the ductus Botalli or ductus arteriosus, with *ap*, the left fifth arch, which becomes the pulmonary artery; the left fourth arch is continued downwards to form the aorta at *ss*; it gives off the left subclavian artery.

The next phase is the increasing complexity of the heart, which doubles upon itself, that portion which is turned to the right, including the curved part, being the ventricular portion, the left and more dorsally situated part being the auricular portion. Each of the four anteaortic arches occupies a visceral fold. The arches unite to form the dorsal aorta, which, after a short course, divides into the common iliacs, each of which gives off an omphalo-mesaraic artery to the yolk sac and capillaries to the tail.

The venous system.—The blood returning from the capillaries distributed over the yolk sac, enters the

omphalo-mesaraic veins, which unite to form a common trunk. The first or most posterior part is called the *ductus venosus*, whilst the part near the auricle is the *sinus venosus*. The object of the first fœtal circulation is the absorption of the yolk, and with the shrivelling

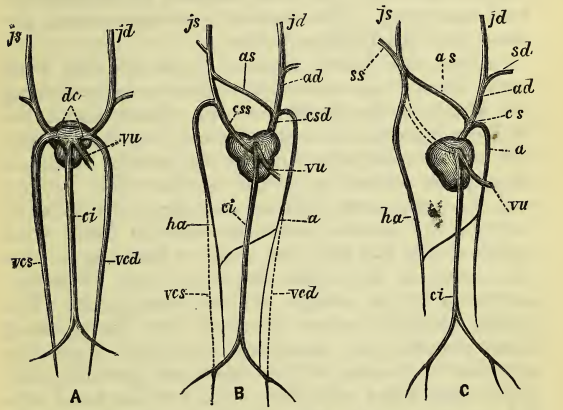


Fig. 41.—Diagram to show the Early Stages of the Second Embryonic Circulation. (Seen from behind.)

js, Left jugular; *jd*, right jugular; *dc*, ductus Cuvieri; *ci*, cava inferior; *vcd*, right cardinal vein; *vcs*, left cardinal vein; *csd*, superior right vena cava; *css*, superior left vena cava; *vu*, umbilical vein; *a*, azygos vein; *ha*, hemi-azygos vein; *ad*, right innominate; *as*, left innominate; *sd*, right subclavian vein; *ss*, left subclavian vein; *cs*, cava superior.

of the yolk consequent on the absorption of its contents, the first circulation disappears. About this time, however, small arteries begin to be distributed to the body of the embryo by the aorta, and the capillaries reunite to form two main trunks on each side, the *jugular* or *anterior cardinal veins* and the *posterior cardinal veins*, which run parallel to the long axis of the body, a little external to the protovertebræ. The two veins of each side soon unite to form a common trunk at

right angles to themselves, which, running inwards, opens into the sinus venosus. These trunks are the *ductus Cuvieri* (*dc*, Fig. 41 A). The jugular or *superior cardinal* vein receives the blood returning from the head and neck, and is soon joined by the vertebral and subclavian veins, returning the blood from the head and wing. The *inferior cardinals* return the blood from the Wolffian bodies.

About the fourth week of fœtal life the vena cava inferior (*ci*) makes its appearance, conveying the blood to the heart from the tissues above the Wolffian bodies; and as these bodies diminish in size, and the true kidneys increase, the inferior cardinals atrophy, as shown in dotted outline (Fig. 41, B), and the vena cava inferior enlarges; the anterior ends of the inferior cardinals unite to form, with others on the left side, the small or *hemi-azygos* vein (*ha*), and on the right the azygos (*a*), which are connected by an oblique communicating vein. The ductus Cuvieri become absorbed into the growing sinus venosus, or, according to some, form the superior venæ cavæ, so that there are now (Fig. 41) three large veins returning blood into the heart, the inferior vena cava, with which the ductus Cuvieri and umbilical vein have coalesced, and the right and left superior vena cava. A new vein estalishes a communication between the right and left jugular veins, and is the rudiment of the future vena innominata sinistra. The left vena cava soon disappears (shown in dotted outline, Fig. 41, C), so that the blood coming from the left jugular vein passes into the now single vena cava superior (*cs*); the portion of the right jugular below the point of opening of the right subclavian vein (*sd*) now becomes the right innominate (*ad*).

Circulation of the fœtus.—It has been shown that in the fowl the first circulation in the embryo was

developed, in order to enable it to absorb the materials for its nutrition, from the vitelline sac; and it was noted, that whilst the extent of this circulation through the omphalo-mesaraic vessels was great in the meroblastic egg, in accordance with the large amount of food yolk it contains, that it was comparatively small and evanescent in the holoblastic egg, on account of the early attachment of the ovum to the uterine walls, from whence it can draw its supply of nutriment by the formation of the chorionic villi with their contained allantoic vessels. These gradually form the placenta, and it is at the placenta that the blood of the fœtus, without intermingling with the blood of the mother, receives by osmosis the pabulum it requires, and gives up the carbonic acid it contains in exchange for oxygen. The necessity that exists for these processes of nutrition and respiration to take place external to the body of the mature fœtus involves some special arrangements of the vascular system, and the course of the blood in the fœtus is as follows:—Commencing at the placenta, aërated and well-nourished blood runs up the single *umbilical vein* to the navel; here it enters the body of the fœtus, and after a short course reaches the liver, where the first special arrangement occurs, for it splits into two parts, one supplying the right and left lobes of the large liver, the other passing through the *ductus venosus*, which lies in the longitudinal fissure of the liver, into the *vena cava inferior*, which also receives the hepatic veins containing the blood that has circulated through the liver. The blood traversing the inferior vena cava enters the *right auricle* of the heart; and here the second special arrangement occurs, for instead of, as in the adult, passing into the right ventricle, it is directed by the Eustachian valve along the back of the auricle to the *foramen ovale*, and immediately enters the *left auricle*. The left auricle contracting

propels it into the *left ventricle*, through the mitral valve, and from them it is driven into the aorta through the sigmoid valves, and is distributed to the head and body as usual. The object of this disposition is apparently to allow aërated blood to reach the head in as pure and highly aërated a condition as possible. The blood returning from the head descends through the jugular and innominate veins into the *superior vena cava*, and from thence into the *right auricle*. This current or column of blood is situated in front of that ascending from the inferior vena cava, and enters the *right ventricle* through the tricuspid valve. When the right ventricle contracts, the blood is driven into the *pulmonary artery* through the semilunar valves; and here the third special arrangement exists, for the lungs are not yet in action, and instead of being distributed to them, as in the adult, it is directed through a channel given off by the left pulmonary artery, named the *ductus arteriosus*, into the aorta, just beyond the point where the left subclavian is given off from that vessel. At this point of the aorta, then, there is a junction of two streams, one which has come direct from the placenta, and is therefore fully aërated, and the other which has traversed the head, and is unaërated. The body generally is supplied with this mixed blood, which, passing through the descending aorta, the common iliacs, and the umbilical artery, reaches the placenta, where it again undergoes aëration, and recommences its course.

As soon as the child is born respiration commences, the lungs become expanded, the pulmonary vessels permit the blood to traverse them freely, and the ductus arteriosus, no longer required, contracts and shrivels, though its remains are always visible. The detachment of the placenta leads to immediate arrest of the flow of blood through the umbilical arteries; no return current consequently takes place through

the umbilical vein; the ductus venosus contracts, the currents of the superior and inferior venæ cavæ mix, and with this the Eustachian valve and foramen ovale become obsolete.

Development of the brain. — The brain is formed from the fore part of the medullary plate, and before the closure of the medullary folds. Two vesicles first appear, and the posterior of these dividing into two make three, known respectively as the fore-, mid-, and hind-brain. The *fore-brain* becomes converted into the cerebral hemispheres, the thalamencephalon, and the primary optic vesicles. The *mid-brain* develops into the optic lobes, or corpora quadrigemina and the crura cerebri; and the *hind-brain* becomes converted into the cerebellum. The brain early presents a remarkable curvature, named the *cranial flexure*, the fore part bending down in front of the extremity of the notochord. Soon after the appearance of this, the *hind-brain*, the cavity of which is the fourth ventricle, becomes divided into two regions: a posterior, the medulla oblongata; and an anterior, the cerebellum. The roof of the medulla becomes

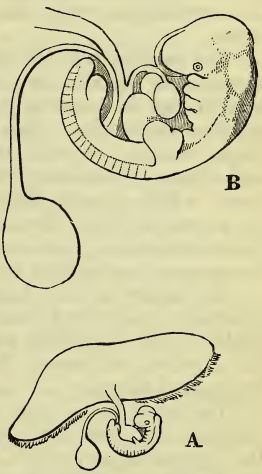


Fig. 42.—Diagram showing the curved Form of the young Embryo: A, natural size, B, magnified. The head is seen to be sharply curved downwards. In the fore and lower part of the head is the eye; immediately below which are the visceral arches. The vitelline sac is seen reduced in size and attached by a long pedicle to the body of the embryo.

attenuated, then breaks down, and the nerves of the two sides, originally in contact at the dorsal summit of the brain, appear to arise at the sides of the brain. The blood-vessels of the pia mater form a plexus over it, which is the choroid plexus of the fourth ventricle. The anterior portion thickens, and becomes the cerebellum, with its central and two lateral lobes.

The *mid-brain* is the single vesicle which has the aquæductus Sylvii for its cavity, with the pons surrounding it posteriorly, and the corpora quadrigemina anteriorly. The *fore-brain* is primarily a single vesicle, but early buds off the optic vesicles, and almost coincidently with them a prolongation in front, which is soon divided off from the fore-brain by a constriction. The posterior part becomes the *thalamencephalon;* the anterior forms the rudiment of the *cerebral hemispheres* and *olfactory lobes.*

The cavity of the thalamencephalon is the third ventricle; posteriorly it is continuous with the ventricle of the mid-brain, and anteriorly it opens into the cerebral rudiment, the aperture becoming the foramen of Monro.

The floor forms anteriorly the optic nerves and chiasma, and posteriorly the *corpora albicantia* and the *infundibulum,* which, coming into contact with an involution from the mouth, gives rise to the pituitary body. The sides of the thalamencephalon thicken to form the optic thalami, which become subsequently united by the grey or middle commissure. The roof forms the pineal gland and the posterior commissure, and a vascular plexus forms above it, which is the tela choroidea of the third ventricle.

The **cerebral hemispheres.**—These develop from the cerebral rudiment of the fore-brain, and gradually attain their predominating size. The floor of

the fore-brain gives rise to the corpora striata, and the roof to the hemispheres, which are separated by a deep groove. The cavity on each side is a lateral ventricle; a septum also forms, from which the falx cerebri is derived. The outer wall of each hemisphere undergoes great thickening, whilst the inner wall becomes thinner, and two curved folds form in it, the upper of which is the hippocampus major, or cornu Ammonis, and the lower gives rise to the choroid plexus of the lateral ventricle. By the fusion of the inner walls of the hemispheres the septum lucidum is formed, which in man is partially separated by a cavity, the fifth ventricle, which has no communication with the true ventricles of the brain. In the anterior part of this septum the fibres of the *anterior commissure* are formed.

The cerebral hemispheres in their primitive state are quite smooth, but there arise a series of convolutions, separated by sulci, which give it a characteristic aspect. The most important, and the first to appear, is the Sylvian fissure, situated at the root of the hemispheres. The part of the brain lying in this fissure is the *island of Reil.*

Development of the cranial and spinal nerves.—The nerves are outgrowths of the central nervous system. The spinal nerves arise from a median and dorsal ridge of cells, named the neural crest, by two lateral outgrowths, which are the rudiments of the posterior roots. The posterior roots are connected by a longitudinal commissure running along the whole length of the neural crest. They develop a ganglion, and shift their point of attachment from the crest to the lateral region of the cord, becoming for a time altogether detached. The anterior roots grow, somewhat later in point of time, from the anterior part of the cord; they have no ganglion, are not united by a commissure, and do not shift their point of attachment. The cranial nerves seem to arise, like

the spinal nerves, from a neural crest, which extends as far as the root of the mid-brain, and is continuous with the crest of the cord. The nerves arising from it are the third, fifth, seventh, and auditory as a single root, the glosso-pharyngeal, and the vagus.

Development of the eye.—The numerous and complicated structures of which the eye is composed are developed in part from the integument of the embryo, partly from the mesoblast, and in part from the central nervous system. It commences with the appearance of the *optic vesicles*, a pair of hollow outgrowths from the anterior cerebral vesicle, the

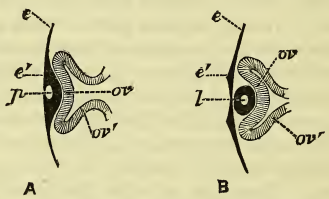


Fig. 34.—A, Early; B, Later Stage of Development of the Eye.

A. *e*, Epiblast thickened at *e'* in front of the optic vesicle, the indented portion of which, *ov*, forms the retina, whilst *ov'* becomes the optic nerve; *p*, cavity in the rudimentary lens. B. The letters have the same signification, but the lens, *l*, is seen to be completely detached, and to lie in the optic cup in contact with the rudiment of the retina.

cavity of which extends into their interior. The stalk elongates, and becomes the optic nerve. The formation of the *lens* and of the *optic cup*, or secondary optic vesicle, now commences. The lens is formed by a thickening of the epiblast, which indents the extremity of the primary optic vesicle, and pushes it back till the front wall of the vesicle is in contact with the posterior wall, and the cavity of the vesicle becomes almost obliterated. The front wall of the cup becomes the retina; the posterior wall, the tesselated pigment layer of the retina. By the closure of the mouth the pit of the involuted epiblast

becomes a completely closed sac; and the lens, separating from the epiblast, forms an oval vesicle with a small central cavity, lying in the pit. Soon, however, a space is formed between the lens and the wall of the cup, which comes to be occupied with the vitreous humour. And now it must be explained, that owing to the obliquity of the position of the optic nerve, which slants downwards, inwards, and backwards towards the vesicle, the lenticular thickening presses in the front wall of the vesicle, not in a line with the axis of the stalk, but in a line forming an obtuse angle with it. The margins of the cup continue to grow up around the lens everywhere, except at the lower part, which corresponds with the stalk, or optic nerve, and here a fissure, the *choroidal fissure*, long remains, which sometimes, instead of closing, remains patent, and constitutes a coloboma of the choroid. The fissure is in the same line as the optic nerve, and through it the mesoblastic tissue, from which the connective tissues within the eye are formed, gains entrance into the cavity of the optic cup. The anterior wall of the optic cup, which it has been said forms the retina, now presents a distinction of parts: the posterior half develops into the true retina; the anterior half becomes the seat of the deposition of pigment, is thrown into folds, covers the ciliary processes, and forms the uvea at the back of the iris. The ciliary processes themselves, with their vessels, the iris, the ciliary muscle, and the vitreous, are all formed from the mesoblast, which has entered the eye through the choroidal fissure. The cornea, which is composed essentially of three layers, the external epithelium, the cornea proper, and the membrane of Descemet, appears to be derived from two sources. The external epithelium proceeds from the epiblast; the internal layer of cells, or membrane of Descemet, and the cornea proper, originate in mesoblast.

Development of the ear.—The auditory vesicle in all vertebrata commences, according to Balfour, with the formation of a thickened patch of epiblast, at the side of the hind brain, on the level of the second visceral cleft. (*See* page 477.) This patch soon becomes invaginated in the form of a pit, to the inner side of which the ganglion of the auditory nerve, which is primitively a branch of the seventh nerve, closely applies itself. The pit closes, and the vesicle so formed retreats from the surface, but remains connected with it by an elongated duct. The inferior part of the sac is produced into a process, which is the rudiment of the *cochlear canal;* the superior part is prolonged into a blind sac, the *aquæductus vestibuli.* The main body of the vesicle becomes the utriculus and semicircular canals, whilst the inferior prolongation forms the sacculus hemisphericus and cochlea. The organ of Corti is developed from the epithelium of the cochlear canal. The Eustachian tube and lymphatic cavity are believed to be derived from the inner part of the hyomandibular, or first visceral cleft. The meatus auditorius externus is formed at the region of a shallow depression, when the closure of the first visceral cleft takes place. The tympanic membrane is derived from the tissue which separates the meatus auditorius externus from tympanic cavity, and presents a hypoblastic epithelium on its inner aspect, an epiblastic epithelium on its outer aspect, and an intermediate mesoblastic layer.

Olfactory organs.—In all the vertebrata the olfactory organs commence, like the eyes and ears, from a pair of thickened patches of epiblast, which, in the case of the olfactory organs, are situated on the under side of the fore-brain, immediately in front of the mouth, and soon become involuted into the form of a pit, the lining cells of which become the olfactory, or Schneiderian, membrane; the surface of the walls

of the pit become greatly increased by foldings. The olfactory nerve attaches itself to the olfactory epithelium at a very early period

Development of the alimentary canal. — The alimentary canal results from the folding in of the splanchnopleure, and is at first straight and parallel to the vertebral column. It is connected with the omphalo-mesaraic duct at a point which corresponds with the lower segment of the ileum, but the duct atrophies, and usually disappears about the fourth month, though a diverticulum sometimes remains persistent. The attachment is at first very broad, and only a thin stratum of mesoblast separates the hypoblast of the canal from the notochord and protovertebræ; but it subsequently attenuates, and becomes the mesentery. In the fourth week the part connected with the umbilical vesicle loops forward. The part above the umbilical opening becomes the small intestine; the part below, almost wholly large intestine; the limit between the two is soon indicated by a projection, the cæcum. The intestine separates from the abdominal wall, the remains of the attachment appearing at the third month, and sometimes later, as a thread-like appendage to the lower part of the ileum. The convolutions then begin to form, and an enlargement in the region of the liver, which is the stomach.

The posterior opening of the intestine is formed by the establishment of a communication between the cloaca, or tube common to the gut and allantois, and a depression on the outside of the body, about the sixth or seventh week. A septum, which is the future perinæum, now grows up, which separates the intestine from the organs forming the allantois.

Various glands arise as outgrowths of the intestinal canal, the mass of the gland being formed of mesoblast, and the lining of the ducts of hypoblast.

Amongst these glands are the salivary glands, the lungs, the pancreas, and the liver. The lungs appear as two hollow vesicles, which give off hollow branches like a gland, and subsequently have a duct or tube common to both, which is the trachea, and the larynx forms at the upper part of the trachea. The epiglottis and thyroid cartilage proceed from the rudiment of the tongue. The large liver commences as a projection formed of two primitive hepatic ducts, which divide and subdivide. At the periphery of the ducts are solid masses of cells, which proceed from the hypoblast. The liver is of large size at the second month, and secretes as early as the third month. The spleen arises in a fold of the mesogastrium at the second month. The adrenals are at first larger than the kidneys.

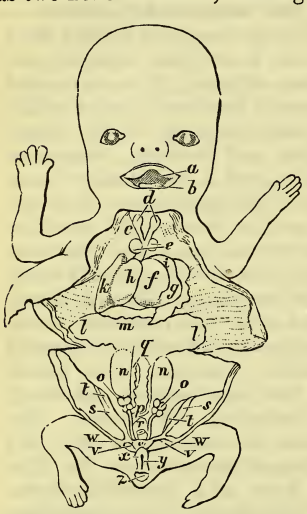


Fig. 44.—Embryo of the Tenth Week. The abdomen has been laid open and the liver and intestines removed.

a, Palatine fissure; *b*, tongue; *c*, carotid of right side; *d*, thyroid body; *e*, thymus gland; *f*, right ventricle; *g*, left ventricle; *h*, right auricle; *i*, left auricle; *k*, right lung; *l*, diaphragm, still membranous; *m*, portion of liver attached to diaphragm; *n*, *n*, suprarenal capsules; *o*, kidneys; *q*, laminæ of mesentery; *p*, ureters; *r*, rectum, divided; *s*, *s*, Wolffian ducts and remains of Wolffian bodies; *t*, *t*, ovaries; *u*, sinus uro-genitalis; *v*, future Fallopian tubes; *w*, future round ligament; *x*, clitoris; *y*, cleft of clitoris; *z*, fold behind anus.

Meconium.—Meconium is the feculent matter contained in the rectum and large intestine of the

new-born child before any food has been taken. It represents the products of the decay of the body during intra-uterine life. The chemical constituents are bilirubin and biliverdin, biliary acids, cholesterin, mucin, traces of formic acid, and other volatile fatty acids, and non-volatile fatty acids. It contains 80 per cent. of water, and about 1 per cent. of ashes (Zweifel).

Genito-urinary apparatus.—The excretory organs of the vertebrata consist of three distinct glandular bodies, and of three ducts :

(1) The *pronephros*, or head kidney, a small glandular body, usually with one or more ciliated funnels

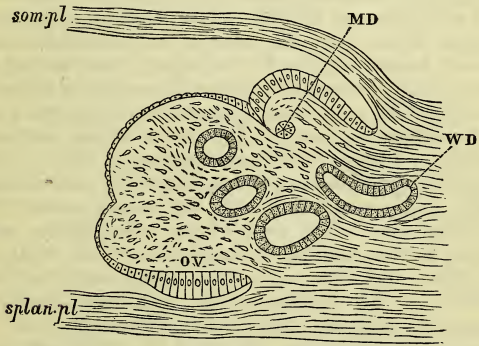


Fig. 45.—Diagram showing First Appearance of Genito-Urinary System.

Som. pl., Somatopleure ; *splan. pl.*, splanchnopleure ; MD, Müllerian duct ; WD, Wolffian duct.

opening into the body cavity, near which is a vascular glomerulus. Its duct, which forms the basis for the generative and urinary ducts, is the segmental duct.

(2) The Wolffian body, or *mesonephros*, consisting of a series of segmental tubes, opening at one

extremity into the body cavity, and at the other into the segmental duct. This duct divides into two, the Wolffian duct and the Müllerian duct.

(3) The kidney proper, or *metanephros*. Its duct is an outgrowth from the Wolffian duct.

In the amniota (reptiles, birds, and mammals) the Wolffian body is a purely embryonic organ and atrophies, whilst the metanephros takes its place and forms the permanent kidney. In the development of each organ the duct is first seen. The first appearance of the *Wolffian duct*, which in mammals is really the homologue of the segmental duct, is a solid rod of cells, primarily derived from the somatic mesoblast of the intermediate cell mass (Fig. 45, *wd*). The solid rod soon becomes tubular. The *Wolffian body* then appears in the form of a series of convoluted tubules, closely resembling the future kidney, commencing in Malpighian bodies with vascular glomeruli and opening into the duct, and the duct opens into the lower part of the alimentary canal. The *duct of Müller* now appears as a furrow, which soon becomes a tube, on the outer surface of the projection formed by the Wolffian body, and opens below into the cloaca, above the Wolffian duct. The duct of the true kidneys now forms, as the result of a constriction of the enlarged Wolffian duct, the new *ureter* lying on the dorsal surface of the Wolffian duct, and soon opening separately into the cloaca. From the upper end of the ureter, diverticula are given off, which are the tubuli uriniferi, and the *kidney* is formed from the mesoblast surrounding them. The ridge of mesoblast at the base of the somatopleure is covered with epithelium of a columnar character, whilst that covering the adjoining portions of the somatopleure and splanchnopleure is tesselated. It is from the proliferation of the *columnar cells*, and of the subjacent fusiform cells of the mesoblast, that the

sexual organs arise, and in both males and females the appearances are identical; large cells, the *primordial ova* proceeding from the columnar epithelial cells lying near the surface of the genital ridge. In males the cells and ova disappear, but in females they enlarge, sink into the stroma, and carry with them some ordinary cells, which unite to form the Graafian follicles. The large nucleus of the primordial ovum becomes the germinal vesicle, while the ovum itself remains as the true ovum (Foster and Balfour).

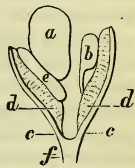


Fig. 46.—Magnified representation of the Urinary and Genital Organs of a Human Embryo eight lines in length.

a, Right suprarenal capsule, completely covering kidney; *b*, left kidney, exposed by the removal of suprarenal capsule; *c*, *c*, ducts representing vas deferens or Fallopian tubes; *d*, ducts of Wolffian body; *e*, testis or ovary; *f*, sinus urino-genitalis.

In males the testes arise in close proximity to the Wolffian bodies, by the formation of tubuli and the growth of the mesoblast. The subsequent changes in the genito-urinary apparatus are, that in birds the *Wolffian body* is converted, in the cock, into the *coni vasculosi* and *epididymis;* in the hen, into parts of the *parovarium.* The *Wolffian duct* remains as the *vas deferens* in the male, and atrophies in the female. The *duct of Müller* remains in the female as the *oviduct*, in the male it atrophies.

Skeleton.—The notochord, probably developed from the hypoblast, is the first rudiment of a skeleton, and occupies the middle line of the body just beneath the medullary canal. It is a cylindrical rod composed of nucleated cells, at first in immediate contact with each other, but subsequently separated by a blastema, or matrix, both cells and matrix being enclosed in a sheath. It reaches at first nearly from one end of the body to the other, but the brain soon begins to extend beyond, and bend over in front of it. In some of the

lower fishes the notochord is persistent, but in higher animals it forms a kind of basis, around which the vertebræ are formed. The vertebræ appear in the form of cubical masses in the vertebral plate on either side of the notochord, and these masses are termed *protovertebræ*. Ossification commences at an early period in the protovertebra as early as the twelfth day in the fowl, the first vertebra to ossify being the second or third cervical, but a portion of each protovertebra remains as a muscle plate and a nerve ganglion. The ribs are developed from the lateral and inferior part of the protovertebra. In man the ossification of the vertebræ begins at the end of the second or the beginning of the third month, with three centres for each vertebra, one for the body, and one for the arch on each side; but these parts do not coalesce till the second year after birth. Accessory centres of ossification are formed at the tips of the spinous and transverse processes, and on the upper and lower surfaces of the bodies. The first appearance of the skull is in the form of a mass of mesoblastic tissue in front of the protovertebræ, which, unlike the vertebral plates, does not undergo any segmentation. This is named the *investing mass*, because it surrounds and invests the end of the notochord, and extends forwards, forming the base of the skull. Its anterior part pushes forth two horns, the trabeculæ cranii, which separate to enclose the pituitary fossa, and reunite in front of it to form the *naso-frontal process*. From the margins of the basal mass, a membranous investment, which soon becomes partly cartilaginous, rises, which covers the brain. The primordial cranial axis, therefore, consists of three parts: a membranous roof; membranous and partly cartilaginous lateral walls; and a cartilaginous base. The several bones are formed by separate points of ossification appearing in these parts.

Development of the skull. — The primitive cranium is membranous, since it is composed of mesoblastic tissue. It is soon replaced, however, by a cartilaginous capsule, which is developed within the membrane. The cartilaginous capsule consists of the three following parts: (1) A pair of cartilaginous plates termed the *parachordals*, at first developed upon either side of the notochord with which they form a continuous plate (known as the basilar plate). This plate forms a floor for the hind and mid brain. (2) The parachordals are continued forwards as two bars of cartilage, *the trabeculæ* basis cranii, which serve as a floor for the fore brain. The trabeculæ are united behind, where they embrace the anterior extremity of the notochord; they then diverge, leaving the pituitary space between them, and afterwards unite and extend forwards into the nasal region. (3) The capsules of the auditory and olfactory organs, the optic capsules usually remaining distinct. From these fundamental parts the adult skull is gradually built up, additional bones being formed by ossification in membrane.

Development of the visceral arches.—At an early period of embryonic life, four visceral or *branchial clefts* appear in the neck of the fœtus as slits extending through the walls of the throat. The anterior border of each cleft becomes raised into a thick *visceral fold*, the posterior border of the last cleft being also raised into a fold, so that the number of folds is five. The visceral clefts and arches, as the folds are subsequently called, usually disappear in the adult. They are homologues of the branchial arches and clefts of Fish. The first and most anterior arch is the mandibular; it is placed in front of the hyo-mandibular cleft. The second arch is the hyoid; it is anterior to the hyo-branchial cleft; the remaining arches and clefts are unnamed. The upper

end of the mandibular arch becomes swollen, and corresponds with the quadrate, whilst the ventral portion constitutes Meckel's cartilage. The hyoid arch divides into two parts, of which the upper forms the incus, whilst the lower remains as the anterior cornu of the hyoid. The incus articulates with the quadrate end of the mandibular arch, which subsequently ossifies as the malleus, whilst its rounded head meets with the stapes, which is segmented from the fenestra ovalis. Meckel's cartilage becomes encased in bone, and forms the basis of the lower jaw. The third arch gives rise to the greater cornua, and to the body of the hyoid bone. The hyo-mandibular cleft constitutes the tympanic cavity.

Development of the face.—The face is mainly developed from mesoblast by an extension of the trabeculæ which meets with the fronto-nasal process growing downwards in the median line, whilst the maxillary and mandibular processes grow laterally. The trabeculæ cranii are continued forwards as a pair of cartilaginous rods, the pterygo-palatine processes, from which are developed the palate bones and parts of the sphenoid. From the median fronto-nasal process the nose is developed ; and from the maxillary process are derived the superior maxillary and malar bones.

The nasal fossæ originate as two depressions in the anterior cerebral vesicles, *the olfactory pits*, at a very early period of embryonic life. *The mouth* commences as a cleft between the maxillary processes and the mandibular arch, its upper border being completed by the fronto-nasal process. The cleft gradually deepens till a communication is established between it and the intestine. The primitive mouth or stomodæum, like the primitive anus or proctodæum, has at first no communication with the primitive intestine. The fauces represent the point of separation between the primitive mouth and the pharynx.

Limbs.—The extremities appear about the fourth week in man in the form of buds from the somatopleure. The arms are the first to appear, and in the first instance no division into fingers or toes are perceptible; a division into upper-arm and fore-arm, and into thigh and leg, is perceptible about the eighth week, but previously to this the extremity of the limb presents indentations indicative of the future digits.

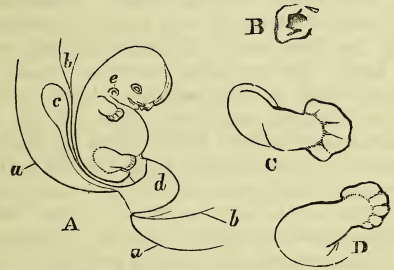


Fig. 47.—Diagram of Formation of Limb.

A, The first appearance of digits formed by slight indentations of the extremities; *a*, *b*, layers of ammon; *c*, umbilical vesicle; *d*, umbilical cord; *e*, ear; B, palmar aspect of hand; C, division of fore from upper arm; D, more advanced stage.

The structures which enter into the composition of the limb are gradually differentiated. The bones first appear as masses of blastema, which develop into cartilage, and in this again points of ossification are formed.

Duration of pregnancy.—Parturition, or the delivery of the child, takes place at the expiration of forty weeks (280 days) from the period of conception. At this period the uterus and its contents have attained a large size, and the act of labour is induced partly owing to the reflex excitation of the genito-spinal centre in the lumbar region of the cord, and partly, perhaps, owing to the direct stimulation of the uterine muscular tissue, and the numerous

ganglia that supply it with motor fibres. A child is viable probably at the commencement of the sixth month.

Physiology of the new-born child.—The act of birth is attended with important organic changes in the fœtus. Respiration commences, often with a cry, and the course of the blood undergoes profound alteration. Before birth, as Preyer well describes the changes, the umbilical vein conveys arterial blood to the liver and heart. After birth the vein becomes obliterated, and forms the round ligament of the liver and obliterated ductus venosus. Before birth the umbilical arteries convey semi-arterialised blood to the placenta. After birth they become obliterated, and form part of the lateral ligaments of the bladder. Before birth the Eustachian valve directs and the foramen ovale permits the passage of oxygenated blood from the inferior vena cava and right auricle to the left ventricle. After birth the Eustachian valve atrophies, and the foramen ovale closes. Before birth the ductus arteriosus conducts arterialised mingled with venous blood from the left ventricle and left pulmonary artery to the aorta. After birth the duct becomes contracted and obliterated. Before birth the lungs are destitute of air, dark red, and contain but little blood. After birth the lungs are filled with air, assume a bright red tint, and contain more blood. Before birth the pulmonary arteries contain mingled arterial and venous blood, coursing from the right ventricle to the lung. After birth they convey only venous blood from the right ventricle. Before birth the pulmonary veins conduct a small quantity of venous blood into the left auricle. After birth they conduct a full current. Before birth the descending aorta conveys mixed blood. After birth the blood is purely arterial. Before birth the inferior vena cava near the heart contains mixed blood. After birth the blood is purely venous.

The immediate cause of the alteration in the direction of the blood, and of the secondary changes in structure that have just been mentioned, is, of course, the change in the blood pressure, for the expansion of the chest and enlargement of the lungs permits a freer current of blood to traverse the pulmonary vessels. The pressure, therefore, is less in the right ventricle and auricle, and the blood finds an easier passage through these vessels than through the foramen ovale into the left auricle. The same explanation may be given of the closure and obliteration of the ductus arteriosus, and the fœtus is born with the lungs unexpanded and the chest in the condition of the most complete expiration. It is in a state of apnœa, the blood being fully charged with oxygen. The act of birth and the contractions of the uterus interfere with the due interchange of gases between the mother and the child, and the circulation of imperfectly arterialised blood through the medulla oblongata at once stimulates the respiratory centres to liberate the motor impulses requisite for inspiration, and the rhythmical sequence of inspiration and expiration is at once commenced. The number of respirations is 44 per minute, and the number of cardiac beats 130. The temperature in the rectum is 37·8° C., but falls during the first few hours 1° to 1·5° C., to rise again to 37·5° C. The circulation through the liver is reduced in activity, owing to the umbilical venous circulation being arrested. The rectum contains meconium. The quantity of urine contained in the bladder is from 8 to 10 cubic centimetres; the quantity of urine discharged in twenty-four hours is from 50 to 60 grammes. The mammary glands often secrete a little milky fluid. Soon after birth hunger is felt, and the child becomes restless, cries, and greedily seizes and sucks the nipple or finger if introduced into the mouth. The cortical motor centres are inactive,

but a light is followed by the eye, and sounds produce a start. The inhibitory action of the vagus is demonstrated with difficulty, and the supervention of death from asphyxia by drowning or suffocation is resisted for a considerable period.

Infancy.—Infancy extends from birth to the eruption of the first teeth, or to about the eighth month; all the vegetative functions of the body are in full activity; the lymphatic and blood-forming organs, as the thyroid, thymus, spleen, and lymphatic glands, are largely developed; the periods of sleep and of waking are about equal; the mental faculties gradually develop; notice is taken of external objects, and the infant can smile and shed tears. The quantity of food taken is considerable; the fæces are yellowish, semi-fluid, without much odour, and contain some unchanged bile, much fat, and coagulated casein. The urine is frequently discharged; its quantity about the fourth month is 300 to 400 grammes. The height augments 30 centimetres in the first year, and the weight of the body is tripled. Some voluntary movements can be performed.

Childhood extends from the first dentition to the beginning of the second dentition, or to about the age of seven years. The number of cardiac beats and of respirations gradually falls. At five years of age the heart's beats are 105; the vital capacity is 900 cubic centimetres; and the respirations are 26 in the minute. During the second year the child learns to walk and speak. Sleep is protracted to nine or ten hours.

Healthy children should grow from 2 to 3 inches a year. They should weigh as nearly as possible to these averages. There is danger if a child falls 7 lbs. below this standard, or grows under 2 or over 3 inches a year.

Arrest of growth and loss of weight indicate malnutrition. They are the frequent forerunners of disease, and should always excite suspicion.

The following is a proportionate table of height and weight:

Height.		Weight.		Height.		Weight.	
Feet	in.	st.	lbs.	Feet	in.	st.	lbs.
2	0	1	4	3	7	3	8
2	1	1	5½	3	8	3	10
2	2	1	7	3	9	3	12
2	3	1	8½	3	10	4	0
2	4	1	10	3	11	4	2
2	5	1	11½	4	0	4	4
2	6	1	13	4	1	4	6½
2	7	2	0½	4	2	4	9
2	8	2	2	4	3	4	11½
2	9	2	3½	4	4	5	0
2	10	2	5	4	5	5	2½
2	11	2	6½	4	6	5	5
3	0	2	8	4	7	5	7½
3	1	2	10	4	8	5	10
3	2	2	12	4	9	5	12½
3	3	3	0	4	10	6	1
3	4	3	2	4	11	6	3½
3	5	3	4	5	0	6	6
3	6	3	6				

Youth.—This period extends from the seventh to the fifteenth year, or to the occurrence of puberty. The milk teeth are shed and the thymus disappears; the bones become firm and solid; the mental faculties are often exceedingly acute, and the memory very exact and tenacious. The vital capacity is about 2,000 cubic centimetres at twelve years of age; the cardiac beats at the same age are about 82. The quantity of urine is about 21 or 22 grammes. The fat of the body is in great part absorbed; and as the period of puberty is reached, the voice alters and becomes deeper, and the conservation of the individual begins to make way for the conservation of the species (Beaunis).

Adult age.—During the earlier period growth

continues, but about the age of twenty, or earlier in women, growth ceases, and for many years the body remains stationary in point of bulk. The faculty of observation and power of acquiring knowledge are active, but at first judgment is defective, and the actions are largely influenced by the emotions. It is from twenty to forty that the most remarkable mental efforts are made, and when genius, if present, usually effects its greatest triumphs. At a later period, though intellectual development may still progress, it is more uniform and sober in its manifestation. In women the period of adult age is interrupted by the occurrence of the menopause.

Old age; senility.—This may be taken to commence about the sixtieth or sixty-fifth year. It is marked by general decay of the bodily powers; the skin begins to be wrinkled, owing to the absorption of fat; the teeth to decay and to be shed; the hair to be white and fall out; the virile power is less active, or altogether ceases; the respirations and the number of cardiac beats are reduced in frequency; the arteries have a tendency to ossify, the veins to dilate; the muscular movements lose their force and precision; the cartilages ossify; the voice alters to "childish treble;" the digestion and the vegetative functions generally are less perfectly performed; the eye is no longer capable of being accommodated to clear vision of near objects, and, with the other senses, loses its acuteness of perception; the mind, however, may long preserve its freshness, and in some instances even seems to mature with advancing age.

Death.—Death, when perfectly natural, occurs as the result of the cessation of the cardiac or respiratory movements, and this is probably the result of inadequate nutrition of the nerve centres governing these acts. In by far the greater number of cases, however, one or other of the vital organs is smitten

with disease, which interferes with the functions of the body at large, and it was from observations of this fact that Bichat maintained that death began at the brain, the heart, or the lungs. To these the kidneys and the intestines might be added. In some instances it is sudden, and scarcely preceded by any appreciable failure of health; whilst in other instances it is prolonged and painful. Beaunis gives the following as characteristic features of the death agony:—The face is livid and sharp-featured; the cheek-bones prominent; the cheeks pendent; the nose sharpened; the forehead covered with a cold, clammy moisture; the eyes dull and unobservant, the lids drooping; the lips livid and discoloured; the mouth partly open; the gums dry, and the teeth covered with sordes; the body inert and yielding to gravity, save only some involuntary movements of the fingers and hands; the extremities cold, the coldness extending gradually upwards; respiration feeble; mucus accumulating in the trachea gives rise to a rattling sound; the cardiac beats, at first frequent, become slower and imperceptible; sensibility is reduced; the eye no longer sees the light; the dying man feels himself to be shrouded in darkness; the hearing often persists to the last; voice fails, and he mutters some incomprehensible words; intelligence may be preserved, but usually fails, and he seems to remember as in a dream some events of his past life; at length the heart ceases to beat, and the last breath is an expiration.

APPENDIX.

A list of some of the more important substances not described in the text, that have physiological relations.

Aceton C_3H_6O.—A colourless mobile neutral fluid; specific gravity 0·792 at 18° C. Its odour resembles that of acetic ether and peppermint. It vaporises easily, boils at 56·3° C., and burns with a slightly smoky flame. It dissolves in water, alcohol, and ether, and acts as a solvent on camphor, fat, resins, and guncotton. It has been found in the urine of patients suffering from *diabetes mellitus*. It is formed by the dry distillation of the acetates, or by the dry distillation with lime of citric, tartaric, and lactic acids, sugar, gum, and starch.

Achroo-dextrin.—An intermediate substance between starch and dextrin, formed by the action of saliva on starch. It does not give any colour reaction on the addition of iodine.

Adipocere.—A compound consisting of lime, palmitate, and stearate. It is found in dead bodies exposed to much moisture.

Allantoin $C_4H_6N_4O_3$.—A product of the decomposition of uric acid. It is found in the allantoic fluid of the calf, and has also been found in the urine of the dog in cases where the respiration has been seriously interfered with for a long time, and in the urine of man after the use of large quantities of tannic acid. It crystallises in thin fascicles, the crystals belonging to the mono-klino-metric system. It is tasteless, and has no action on litmus. It dissolves at 20° C. in 160 parts, at a boiling heat in 30 parts of water, and more easily in spirit of wine. It is an anhydride of 2 molecules of urea $2(N_2COH_4)$ and glyoxylic acid $C_2H_4O_4$. Acids and alkalies split it into urea and allanturic acid.

Alloxan $C_4H_2N_2O_4$.—A substance having close relations with uric acid, from which it can be obtained by oxydation. It crystallises with 4 equivalents of water of crystallisation in large brilliant rhombic pyramids, which effloresce when exposed to air. It dissolves easily in alcohol and in water. The watery solution stains the skin of a purplish colour, and communicates

a disagreeable odour to it. It has an acid reaction, and disagreeable taste. With salts of iron, it gives a dark indigo blue colour. It is a powerful oxydising agent.

Asparagin $C_4H_8N_2O_3$.—The amide of aspartic acid; a substance obtained from the turios of asparagus, but also contained in symphytum officinale (comfrey), convallaria majalis (Solomon's seal), and Paris quadrifolia (herb Paris), and in the seeds of leguminous plants. It forms colourless and odourless transparent stable crystals, belonging to the rhombic system. It dissolves in 58 parts of water at 13° C., and in 4·5 parts of boiling water. It is quite insoluble in alcohol at all temperatures, in ether, and in oils.

Aspartic acid $C_3H_7NO_2$.—It is formed by the decomposition of asparagus under the influence of alkalies; also by the decomposition of proteids, such as legumin, egg albumin, and casein, by means of sulphuric acid. By fermentation or putrefaction, aspartic acid is converted into succinic acid.

Carnin $C_7H_8N_4O_3 + H_2O$.—This substance is contained in Liebig's extract of meat, in which it exists in the proportion of about one per cent. It is allied to sarkin, into which it can be converted with loss of H and CO_2 by the action of bromine or chlorine, with a little nitric acid.

Cerebrin.—This substance is only found in nerve-tissue and in pus cells. It forms a delicate white tasteless powder, destitute of smell, and composed of rounded granules. When heated to 80° C., it becomes brown, then, at a higher temperature, forms bladders and decomposes. When in a somewhat impure form, and containing some lecithin and cholesterin, it gives the appearance of myelin drops, or double-bordered intestine-like clumps, which prolong themselves into long threads, and refract light strongly. Solutions of cerebrin do not act on litmus paper. When boiled with acids it yields a kind of sugar, that rotates polarised light to the left, but does not ferment.

Cheno-taurocholic acid.—An acid found in the bile of the goose.

Cholalic acid $C_{24}H_{40}O_5$.—A product of the decomposition of glycocholic acid with absorption of water at a boiling temperature, glycocol being separated at the same time.

$$\underset{\text{Glycocholic acid}}{C_{26}H_{43}NO_6} + H_2O = \underset{\text{glycocol}}{C_2H_5NO_2} + \underset{\text{cholalic acid.}}{C_{24}H_{40}O_5}$$

Cholesterin $C_{26}H_{44}O + H_2O$.—This substance is best obtained from gall stones, which are in great part composed of it. Anhydrous cholesterin crystallises out of benzol, chloroform, or pure ether, in fine colourless silky needles. Hydrated

cholesterin crystallises out of boiling alcohol in microscopic oblique rhombic plates. It is insoluble in water, alkalies, and diluted acids, and with difficulty in cold alcohol, but very easily in hot ether or boiling alcohol, chloroform, benzol, volatile oils, and fatty acids. Anhydrous cholesterin melts at 145° C., and distils unchanged in vacuo at 360° C. Concentrated sulphuric acid converts it in the cold into a red mass, which, on the addition of water, becomes green. On account of its forming ether-like compounds with one molecule of acid, which are saponifiable by alcoholic solution of potash, it is regarded as a univalent alcohol.

Cholin $C_2H_{15}NO_2$.—A product of the decomposition of lecithin; it does not appear to be a constituent of the body. It is a thick syrup, easily soluble in water and in alcohol; it turns litmus paper blue. (*See* under LECITHIN.)

Dyslysin $C_{24}H_{36}O_3$.—This substance is the ultimate product of the action of boiling hydrochloric acid upon glycocholic acid or upon cholalic acid.

$$\underset{\text{Glycocholic acid}}{C_{26}H_{43}NO_6} = \underset{\text{glycocol}}{C_2H_5NO_2} + \underset{\text{dyslysin}}{C_{24}H_{36}O_3} + \underset{\text{water.}}{H_2O}$$

It is a white amorphous tasteless mass, soluble in ether, with more difficulty in alcohol, and scarcely at all in water, alkalies, acetic or hydrochloric acids. It melts at 140° C., and burns with a smoky flame.

Formic acid CH_2O_2.—An acid obtained, as its name implies, from ants, but present also in many plants. It has been found in blood, in urine, milk, sweat, and in the juice of muscle of man.

Glycerin $C_3H_8O_3$.—A secondary product obtained by the action of superheated steam upon fats. It has not been shown to be a constituent of the body. It is without colour or odour, but has a burning sweet taste, is of oily consistence, has a neutral reaction and a sp. gr. of 1·26. It boils at 290°, and the vapour ignites, burning with a feeble but not smoky flame; at −40° it becomes a gummy mass, but does not crystallise; on withdrawal of water by rapid boiling condensed glycerin-molecules are formed, such as diglyceride and polyglyceride. Placed in contact with yeast it yields propionic acid $C_3H_6O_2$. With chalk and putrefying cheese it yields at 40° C. butyric acid $C_4H_8O_2$ and ethyl alcohol C_2H_6O. By long heating of glycerin with excess of fatty acids in hermetically sealed tubes at a temperature of 200° to 270°, triglycerides are produced, which are identical with the ordinary fats. The oxydation of glycerin by means of nitric acid yields tartaric acid, and when heated with potassium hydroxyl to a temperature of 200° C., potassium

formiate and potassium acetate are produced. Glycerin is a trivalent alcohol. It is intimately associated with acetone, acrolein, and the allyl series generally, and consequently with the propyl series of compounds.

Glycerin-phosphoric acid $C_3H_5(OH)_2,O,PO(OH)_2$.—An acid syrup, which, when slightly warmed, breaks up into glycerin and phosphoric acid. It is a bibasic ether acid, which combines with bases to form crystallisable salts. Easily soluble in water, but soluble with difficulty in alcohol. It is a product of the decomposition of lecithin.

Hypoxanthin $C_5H_4N_4O$.—A constituent of muscle, in which it is found in the proportion of 0·02 per cent. It may be obtained by acting on xanthin or uric acid with sodium amalgam. The relation between these organic substances is immediately apparent on considering the following formulæ:

$C_5H_4N_4O$	,	$C_5H_4N_4O_2$	,	$C_5H_4N_4O_3$
Sarkin		xanthin		uric acid.

Indican $C_{26}H_{31}NO_{17}$.—The quantity of indican excreted in the urine of man is very inconsiderable; it is most abundant on meat diet. It can be obtained in larger quantities from the urine of the horse. It appears in the form of a bright brown strongly odorous syrup, of bitter and nauseous taste, which has a neutral reaction, and is precipitated by lead acetate. It is not altered by dilute sulphuric acid or by alkalies. Acidified solution of indican with a trace of chlorine gas gives a blue colour from the formation of indigo. The indican contained in urine is not identical with that in the plant named *Isatis tinctoria*. When acted on by concentrated acid, leucin, volatile fatty acids and a purplish red body named urrhodin are formed. When its aqueous solution is treated with hydrochloric acid in presence of oxygen, it yields indigo blue.

Indigo.—A crystalline blackish-blue powder, consisting of needles or oblique rhombic plates, the surface of which has a copper-red metallic glint. Indigo is insoluble in water, alcohol, ether, alkalies, and dilute acids, but is easily soluble in boiling chloroform, amyl-alcohol, and melting paraffin. When dissolved in amyl-alcohol its spectrum presents between *d* and D a dark absorption band.

Indol C_8H_7N.—A substance crystallising in large pearly thin tablets of peculiarly offensive odour. It melts at 52° C., and volatilises unchanged *in vacuo* at 218° C. It is soluble in water. The dilute solution on the addition of chromic acid gives a dark violet very voluminous precipitate, which is insoluble in ether, chloroform, and benzol, but is soluble in alcohol with a red tint, and in hydrochloric acid with a violet

colour. It is one of the final products of the action of pancreatic juice on proteids, and it may also be obtained by the distillation of proteids with the caustic alkalies.

Inosinic acid $C_{10}H_{14}N_4O_{11}$.—An acid obtained in the proportion of about 0·01 per cent. from the muscles of cats and rabbits, but not certainly from that of other mammals, and in the proportion of about 0·02 per cent. from the muscles of the goose, duck, and pigeon; it has a taste and an odour resembling that of broth, and appears in the form of a syrup from which, on the addition of bases, crystalline salts can be obtained.

Inosite $C_6H_{12}O_6 + 2H_2O$.—Muscle sugar or phaseomannite, found in muscles and in various fruits of the leguminosæ. It forms large colourless monoklinic tabular crystals. It is soluble in six parts of water at 19° C. It is incapable of undergoing fermentation, and does not reduce alkaline solution of copper sulphate, nor does it exert a rotatory action on light. When moistened with a little nitric acid and evaporated to dryness, and then mixed with ammonia and calcium chloride, it gives a rose colour; when placed in contact with putrefying cheese it yields propionic, butyric and paralactic acids.

Keratin.—A substance of inconstant composition obtained after the successive action of boiling water, alcohol, ether, and dilute acids on various epidermoid tissues, as upon fish scales, nails, horn, hoofs, feathers, and the epidermis. It is insoluble in alcohol and ether, swells up in hot water, and still more easily in acetic acid; it does not undergo putrefaction; melts when heated, and burns with a luminous smoky flame, having a peculiar odour. Boiled with dilute sulphuric acid or with hydrates of alkalies, it yields aspartic, acetic, butyric, propionic, and valerianic acids, with ammonia, leucin, and tyrosin; treated with nitric acid it yields oxalic acid as a terminal product.

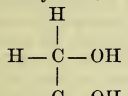
Kreatin $C_4H_9N_3O_2 + H_2O$.—A substance found in the muscles of all vertebrata. It crystallises in colourless oblique rhombic prisms, readily soluble in hot water. Soluble in 9400 parts of alcohol, and insoluble in ether. It has a bitter taste. Boiled with baryta water it breaks up in urea and sarkosin, taking up one equivalent of water. Kreatin is an intermediate product of the disintegration of muscle and nerve tissues. It is not found in gland tissue. Heated with mercuric oxide it yields oxalate of methylguanidin, which establishes a relation between it and guanin.

Kreatinin $C_4H_7N_3O$.—A substance found in the urine. It can be artificially made by boiling kreatin for four or five days with concentrated acids, when it gives up one equivalent of water and becomes converted into kreatinin. Kreatinin

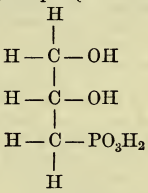
crystallises in long colourless monoklinic prisms, which are soluble in 100 parts of cold alcohol, and in 11·5 parts of cold water. The solution turns litmus paper blue.

Lecithin $C_{44}H_{90}NPO_9$, or $C_{42}H_{84}NPO_9$.—A constituent of the brain and of yolk of egg. It crystallises in fine needles on slow cooling of its alkaline solution. It swells up like starch on the addition of water. It dissolves with difficulty in cold alcohol and in ether, but easily in chloroform, benzol, boiling alcohol and ether, and in hot acetic acid. Lecithin is a glycero-phosphoric acid, of which the alcoholic hydroxyls have exchanged their H for a radical of a fatty acid, which may either be oleic, stearic, palmitic, or some other, and in which one atom of the phosphoric acid is replaced by the powerful organic base named neurine or chlorine. The graphic formula is thus given by Nuel:

Glycerine.

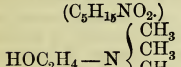


Glycero-phosphoric Acid.

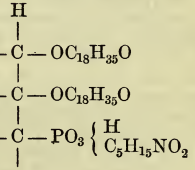


Cholin or Neurine.

$(C_5H_{15}NO_2.)$



Lecithin.



Leucin $C_6H_{13}NO_2$. — This is identical with amido-capronic acid. It appears in the form of crystalline lamellæ, or minute spheroids, which are almost insoluble in water, but are moderately soluble in alcohol. When heated to 170° C., leucin sublimes, giving forth an odour of amylanine. The presence of leucin can be recognised by Scherer's test, which consists in heating it on a platinum spatula, when it leaves a colourless residue. This, heated with a drop or two of soda

solution, assumes a yellow or brown tint, and on the further application of heat becomes converted into an oily drop, which rolls over the surface of the platinum without adhering to it.

Lutein.—This substance forms microscopic red crystals insoluble in water, soluble in alcohol, ether, chloroform, benzol, and fat oils. On the addition of nitric acid it becomes green, blue, yellow, and then colourless. It is thought to be identical with hæmatoidin.

Malic acid $C_4H_6O_5$. — An acid widely distributed amongst plants, often in association with tartaric and citric acid; thus it is found in apples, cherries, pine-apple, tamarinds, in aniseseed, in the berries of the mountain ash, and in rhubarb. The crystals melt at 83° C. When ingested into the stomach the malates are decomposed, and appear in the urine in the form of carbonates and bicarbonates of the alkalies.

Mucin.—A substance which may be procured from the salivary glands and from the snail. It forms a white or yellowish substance insoluble in water, but capable of swelling up when immersed in it. It does not diffuse through animal membranes. It is immediately precipitated on the addition of alcohol, to a mixture of water and mucin. It is soluble in concentrated acids and alkalies. It does not coagulate on boiling, it is not precipitated by metallic salts excepting basic acetate of lead, or by potassium ferrocyanide, or by tannic acid. It gives a rose-red colour with Millon's reagent, and a yellow colour with nitric acid.

Myosin.—Muscle, when frozen and thawed, retains its irritability, and therefore undergoes no material chemical alteration. As a result of these processes, if muscle be cleared of blood by injection of 0·75 per cent. solution of common salt, and cleaned from other tissues, it may be frozen and powdered. A little below 0° C. it becomes syrupy, and on filtration a syrupy liquid passes through the filter, which is the plasma of muscle. This coagulates a little above 0°, yielding a clot named myosin, and a clear yellowish fluid named "muscle serum." It coagulates slowly at 0°C., rapidly at 40° to 50°, or on dilution with water, or on the addition of an acid. Myosin resembles the globulins. It is insoluble in water, soluble in a dilute solution of sodium chloride, ammonium chloride, or magnesium sulphate. Myosin is not a constituent of muscle, but is generated in muscle after death, just as fibrin is formed after blood has been withdrawn from the vessels. It is converted into syntonin by acids, and syntonin can be reconverted into myosin by the successive action of lime-water, ammonium chloride, and acetic acid.

Neurin. (*See* under Lecithin.)

Nuclein.—A substance obtained from the nuclei of cells. It may be obtained from pus cells by digesting them in warm alcohol to remove fat and lecithin; on the addition of gastric juice the albumin of the cells is converted into peptones, and dissolved when the nuclei, which resist the action of the gastric juice, gravitate to the bottom of the vessel; and they are then further purified from fat and lecithin by the successive application of ether, cold water, and alcohol. Pus cells dried at 110° C. contain 33 per cent. of nuclein.

Paralactic acid $C_3H_6O_3$.—An acid that, notwithstanding its alkaline reaction, seems to be present in muscle; during muscular effort it accumulates in the tissue to such an extent as to confer upon it an acid reaction. It is of syrupy consistence, and mixes with alcohol, ether, and water. It is monobasic. It rotates a ray of polarised light to the right.

Phenol C_6H_6O is found in the urine in the form of a conjugated sulphur acid (phenosulphuric acid) combined with potassium. Phenosulphate of potassium crystallises in brilliant white scales, soluble in water, almost insoluble in alcohol. Acids decompose it into phenol and sulphuric acid. When rapidly heated it melts, dissolves in water, and assumes a red tint on the addition of perchloride of iron.

Pyrocatechin $C_6H_4OH_2$ is an occasional constituent of the urine, either pure or in conjugation with sulphuric acid. In this case the urine on standing acquires a deep brown shade in its upper layers, and becomes of a blackish brown tint on the addition of alkalies. It reduces ammoniacal solutions of silver nitrate, mercury nitrate, and copper sulphate. In watery solution pyrocatechin gives an emerald green colour with perchloride of iron, which becomes violet on the addition of tartaric acid and ammonia.

Sarkin.—The same as Hypoxanthin.

Sarkosin $C_3H_7NO_2$.—An amido-acid-methyl-glycocol, not certainly ascertained to be a constituent of the body, but interesting as being a derivative of kreatin, for when this substance is boiled on by baryta water, it yields ammonia and barium carbonate, and sarkosin can be obtained by evaporation of the liquid. Caffein treated in the same way also yields sarkosin. It crystallises in colourless rhombic prisms, easily soluble in water, less so in alcohol, and not at all in ether. It has a burning sweet taste.

Skatol C_9H_9N.—A white crystalline substance, of peculiarly offensive fæcal odour, which is less soluble in water than indol. Its watery solution gives a milky cloud when mixed with a few drops of fuming nitric acid.

Succinic acid $C_4H_6O_4$.—An acid found in small quantities in several animal fluids, but usually obtained artificially. It forms colourless monoklinic prisms, or microscopic six-sided tablets, soluble in three parts of boiling, and 17 parts of cold water; specific gravity 1·552. It begins to sublime at a temperature of 120° C., melts at 180°, and boils at 235°, decomposing into anhydride and water. The vapour tastes acid, and excites cough. It stands in genetic relation with the fatty acids, as the butyric and valerianic, and with the fats with fumaric and maleic acids, with the glycerin-acids, and with some organic acids, as the malic and tartaric.

Tyrosin $C_9H_{11}NO_3$.—An aromatic compound obtained by boiling horn shavings, or any of the proteids, with sulphuric acid, neutralising with lime-water, and, after filtration, adding lead acetate to the filtrate, when tyrosin-lead is formed. The tyrosin is set free by the addition of sulphuric acid. It forms white silky needles on crystallising, which are insoluble in ether and alcohol, soluble in 1900 parts of cold water, and easily soluble in dilute acids and alkalies, with the exception of acetic acid. Solution of tyrosin heated with mercury nitrate turns of a rose colour. Tyrosin may be regarded as one of the products of the oxydation of all proteid bodies, or of their putrefaction or regressive metamorphosis. It is an alanin in which H is substituted by oxy-phenyl C_6H_4OH. Dissolved in hot concentrated sulphuric acid, it gives a rose colour to the liquid. (Piria's reaction.)

Xanthin $C_5H_4N_4O_2$.—An amorphous powder of yellowish-white colour, or crystalline lamellæ, slightly soluble in water, insoluble in alcohol and ether, and soluble in caustic ammonia. Heated with nitric acid, it gives a yellowish residue, which, on the addition of soda, assumes a red colour, and becomes purple when heated. It forms crystallisable salts. It may be obtained artificially by the action of nitrous acid upon guanin. Caffein (trimethylxanthin), and theobromin (dimethylxanthin), can be prepared from it synthetically.

Zoamylin.—The same as GLYCOGEN.

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